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A. GENERAL TEXTBOOK OF ENTOMOLOGY

INCLUDING THE ANATOMY, PHYSIOLOGY, DEVELOPMENT AND CLASSIFICATION OF INSECTS

BY

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FORMERLY FOREST ZOOLOGIST TO THE GOVERNMENT OF INDIA

WITH 624 ILLUSTRATIONS

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PREFACE

IN undertaking this textbook the author has attempted what is unquestionably a severe test of his comprehension of his subject. A task of this kind reveals, perhaps better than any other, how difficult it has now become for a single individual to deal adequately with the different specialized branches of entomology. The book is the outcome of a number of years' experience of the need of a treatise which will meet the requirements of the research worker, the advanced student and the teacher. Its aim has been to present the chief facts concerning the structure, physiology, development and classification of the Insecta and the biology of their more important representatives. The treatment of an extensive subject like entomology is largely a process of compression, in order that the volume may be kept within reasonable compass. The attainment of this latter object has made it imperative to make only brief reference to problems of insect behaviour, ecology, coloration, cytology, etc., while the extensive branch of palæontology has been omitted.

The author has attempted to do justice to the great mass of knowledge which the activities of a host of investigators have accumulated during recent years. Much material has been introduced which has not previously appeared in textbooks, and the bibliographies are mainly arranged at the end of each section concerned, but a certain number of references are included, for the sake of brevity, in the text. The object throughout the book has been to present before the reader essentials but, at the same time, to indicate where fuller information is available. The question of generic and specific names is a perennial bone of contention and endeavour has been made to use those as up-to-date as possible. At the same time, it has not been deemed advisable to adopt the most recent and unfamiliar mutations of nomenclature.

Throughout Part III, which deals with the orders of insects, reference is made to species of economic significance with short accounts of their habits. The subject of applied entomology has assumed paramount importance in relation to agriculture, forestry, medicine and other aspects of human welfare. Separate textbooks are available dealing individually with those several branches. Experience, however, has taught us that success in any branch of applied science is dependent upon a thorough grasp of the principles of that science. In this connection, therefore, it is hoped that the present work will also be found of value to the many workers in applied entomology scattered throughout British dominions.

Acknowledgments are due to the Chief of the Division of Publications, U.S. Dept. of Agriculture and to the U.S. National Museum for permission to reproduce a number of illustrations. The author is also much indebted to Prof. J. H. Comstock for the use of figures from his *Wings of Insects* and *Introduction to Entomology* and for kindly supplying electrotypes. Prof. W. M. Wheeler has granted the use of illustrations from his work on Ants and Prof. J. W. Folsom has extended similar facilities with reference to the last edition of his *Entomology*. Thanks are also due to the publishers of those works, the Columbia University Press and P. Blakiston's Sons and Company, respectively, for their consent. Sir Arthur Shipley and Dr. H. Scott have granted facilities for using a number of illustrations from *The Fauna of British India* and Mr. W. Foster of the India Office courteously made arrangements for providing the necessary electrotypes: figures borrowed from this source are indicated thus—(F.B.I.). Messrs. Longmans, Green and Co. allowed the use of three figures from Schafer's *Essentials of Histology* and Messrs. George Allen and Unwin allowed blocks to be made of several of the illustrations from the English edition of Korschelt and Heider's *Textbook of Embryology*. The Princeton University Press allowed the copying of two figures from Nelson's *Embryology of the Honey Bee* and the Cambridge University Press supplied blocks from Tillyard's *Biology of Dragonflies* and Latter's *Natural History of some Common Animals*. Mm. Masson et Cie. granted the use of three illustrations from Henneguy's *Les Insectes* and an illustration from Brumpt's *Precis de Parasitologie*. Messrs. A. & C. Black consented to the use of two figures from Curtis' *Farm Insects* and Mr. John Murray supplied a block from Darwin's *Descent of Man*. Thanks are also due to the Clarendon Press for the use of illustrations from Miall and Hammond's work on Chironomus while Fig. 556 is taken from Cheshire's *Bees and Beekeeping* by consent of the publishers. Messrs. Macmillan & Co. allowed the use of illustrations from the *Cambridge Natural History* and from Sladen's *Humble Bee,* and the director of the *Faune de France* kindly allowed two figures to be copied from that publication.

The author is especially indebted to Mr. J. E. Collin for the loan of a number of the admirable drawings made for Verrall's great work on British Diptera. Acknowledgments are due to Prof. Bugnion for the loan of blocks and the use of several of his published figures; also to Messrs. W. J. Lucas and H. Main for several photographs.

Thanks for the use of illustrations are also due to Prof. A. Berlese, Prof. L. Bordas, Dr. F. Brocher, Dr. G. H. Carpenter, Dr. G. Grandi, Prof. R. Heymons, Dr. D. Keilin, Dr. A. Lecaillon, Prof. P. Marchal, Prof. T. H. Morgan, Prof. G. H. F. Nuttall, Major W. S. Patton, Prof. C. Pérez, Prof. F. Silvestri, Prof. J. M. R. Surcouf, Dr. R. J. Tillyard, Dr. C. L. Withycombe and many others. In every case acknowledgment is made to the author beneath each borrowed illustration.

The author is also indebted to Mr. H. M. Morris for assistance in drawing or otherwise preparing a considerable number of the illustrations. Mr. Morris also carried out many dissections, etc., under the author's direction and great credit is due to him for his skill in these matters. Other of the illustrations were drawn by Miss E. Salisbury, Mr. A. M. Altson, Miss A. Mardall and Miss O. Tassart. Dr. W. E. Brenchley has rendered invaluable aid in the heavy task of reading through the manuscript and proofs. Acknowledgments are also due to Dr. J. Davidson, Mr. E. E. Green and Mr. J. G. H. Frew, more especially for help in their special branches, and to Mr. A. N. Caudell for the loan of a winged example of the Zoraptera.

A. D. IMMS

ROTHAMSTED EXPERIMENTAL STATION
HARPENDEN
September, 1924

PREFACE TO SECOND EDITION

THE necessity for issuing a second edition, in a comparatively short interval of time, is taken as an indication that this book has fulfilled a definite requirement. The labour of revision has been considerable, and sincere thanks are due to those entomologists in various parts of the world who lightened the task by their comments upon individual paragraphs, or sections of several of the chapters. In more than one instance the reviewers' criticisms have also proved helpful.

In the second edition various additions and emendations have been made. The most important are the revised classifications affecting the orders Dermaptera, Isoptera and Thysanoptera : the supplementary literature at the end of many of the chapters : and the notes on recent advances in the subject incorporated in the Addenda on pp. 668–72. One new diagram has been added and three of the text-figures have been replaced by new illustrations. Special thanks are due to the McGraw-Hill Book Company, of New York, who allowed the use of an illustration from *The Anatomy and Physiology of the Honey Bee*, by Snodgrass.

The perennial subject of taxonomic nomenclature is always a difficulty in a book of this description. In reply to criticisms by specialists it may be pointed out that the latest names in many cases have not been adopted, but rather those which are best known and most widely used.

The author desires to express his appreciation of the courtesy he has received from Messrs. Methuen & Co. in meeting his wishes in matters affecting the production of this volume.

A. D. IMMS

ROTHAMSTED EXPERIMENTAL STATION
HARPENDEN
October, 1929

PREFACE TO THIRD EDITION

THE preparation of a third edition of this textbook has entailed considerable revision. Much of the portion dealing with anatomy and physiology has been emended or rewritten in order to bring it in line with recent ideas and discoveries. In the chapter on Orthoptera a section has been added concerning the phases of locusts. The Dermaptera have been more fully classified and a detailed family synopsis has been appended to the Ephemeroptera. The classification of the Lepidoptera has been partially recast and fuller treatment given to the extensive group of the Tineoidea. Considerable revision has been undertaken with regard to the Symphyta, Cynipoidea and Vespoidea ; the Masaridæ and the Eumenidæ, it may be added, are now included in the single family Vespidæ. The Diptera have been reclassified in so far as three sub-orders are recognized, the old and somewhat unnatural assemblage of the Orthorrhapha being no longer retained : the Calypteræ have also been regrouped more in accordance with recent taxonomy. Various minor additions or emendations require no special mention. A number of supplementary references to the literature are given, and certain of the older citations omitted. Some 37 new illustrations have been included and, of these, 20 replace figures that have done duty previously, while the remainder are additional.

Thanks of the author are again due to those entomologists who have sent critical remarks or corrected minor errors. Particular mention needs to be made of assistance given by Mr. R. E. Snodgrass, of Washington, D.C., who generously allowed use to be made of some of his unpublished researches. Grateful acknowledgment is also due to Professor J. Stanley Gardiner, F.R.S., who placed the services of an artist at the author's disposal in connexion with the production of new text-figures. Finally, the author wishes to acknowledge the courtesy received from Messrs. Methuen & Co. during the preparation of this edition.

A. D. IMMS

ZOOLOGICAL LABORATORY
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A GENERAL TEXTBOOK OF ENTOMOLOGY

Part I

ANATOMY AND PHYSIOLOGY

INTRODUCTORY REMARKS

Definition of the Insecta (Hexapoda)

THE members of this class are tracheate Arthropods in which the body is divided into head, thorax and abdomen. A single pair of antennæ (homologous with the antennules of the Crustacea) is present : the thorax carries three pairs of legs and usually one or two pairs of wings. The abdomen is devoid of ambulatory appendages, and the genital opening is situated near the anal extremity of the body. Post-embryonic development is rarely direct and a metamorphosis is usually undergone.

Relationships with Other Arthropods

The Arthropoda constitute the largest phylum of the animal kingdom and, although they include animals differing widely in structure, they agree in certain fundamental characters. The body is segmented and invested with a chitinous exoskeleton. A variable number of the segments carry paired jointed appendages exhibiting functional modifications in different regions of the body. The heart is dorsal and is provided with paired ostia, a pericardium is present and the body-cavity is a hæmocœle. The central nervous system consists of a supra-œsophageal centre or brain connected with a ganglionated ventral nerve cord. The muscles are composed almost entirely of striated fibres and there is a general absence of ciliated epithelium. No animals other than Arthropods exhibit the above combination of characters. The various classes of the phylum are as follows.

The **Onychophora** (Peripatus) are in some respects annectent between the Annelida and Arthropoda, but the reason for their inclusion in the latter phylum is not evident from superficial examination. They are perhaps to be derived from Polychæte ancestors which had forsaken a marine habitat and become terrestrial. Parapodia are consequently no longer present as swimming organs, but have become modified for locomotion on land without having acquired the jointed Arthropod character. The integument is soft, no chitinous exoskeleton being developed, and the excretory organs take the form of metamerically repeated nephridia. Arthropodan features are exhibited in the possession of tracheæ, salivary glands, and the terminal claws to the appendages. The presence of jaws of an appendicular nature, the paired ostia to the heart, the pericardium, the hæmocœlic body-cavity and the reduced cœlom are further important characters allying them with that phylum.

The **Trilobita** (Trilobites) are an extinct class of palæozoic marine forms with the body moulded longitudinally into three lobes. They possess a single pair of antennæ followed by a variable number of pairs of biramous limbs little differentiated among themselves. Four pairs of these appendages belong to the head and the remainder to the trunk region.

The **Crustacea** (Lobsters, Shrimps, Crabs, Barnacles, etc.) are characterized by the possession of two pairs of antennæ and at least five pairs of legs. In the higher forms the body segments are definite in number and arranged into two regions—the cephalothorax and abdomen. Respiration almost always takes place by means of gills, and the excretory organs are highly modified nephridia usually represented by green glands or shell glands. The genital apertures are situated anteriorly, i.e. on the 9th post-oral segment in some cases, up to the 14th in others.

The **Arachnida** (Scorpions, King Crabs, Spiders, Mites, Ticks, etc.) are distinguished by the body usually being divided into cephalothorax and abdomen ; the legs consist of four pairs and there are no antennæ. The primitive forms respire by means of brancheæ which, in the higher forms, are insunk to form lung-books, or atrophied and replaced by tracheæ. Spiracles when present are generally abdominal and consist at most of four pairs. The gonads open near the base of the abdomen and the excretory organs are usually Malpighian tubes. The presence of cheliceræ, in place of sensory antennæ, and the general characters of the remaining appendages mark off the Arachnida very definitely from all other Arthropoda.

The next four classes (often known collectively as the Myriapoda) are characterized by the presence of a single pair of antennæ and the absence of any differentiation of the trunk into thorax and abdomen. Each segment usually bears appendages.

The **Diplopoda** (Millipedes) have the greater number of the body segments so grouped that each apparent somite carries two pairs of legs and two pairs of spiracles. The gonads open behind the 2nd pair of legs.

The **Pauropoda** are characterized by the legs being arranged in single pairs although the terga are mostly fused in couples. The antennæ are biramous and there are only twelve post-cephalic segments, nine of which bear legs. The gonads open on the third segment.

The **Symphyla** have long antennæ and most of the body segments bear a single pair of legs. The gonads open on the fourth post-cephalic segment and there is a single pair of spiracles which are situated on the head.

The **Chilopoda** (Centipedes) are usually provided with a single pair of appendages and a pair of spiracles to each of the post-cephalic segments. The first pair of legs is modified to form poison claws and the gonads open on the penultimate segment of the abdomen.

The **Tardigrada** (Bear Animalcules) are very minute animals with four pairs of unjointed legs but devoid of antennæ, mouth-appendages or respiratory organs. The gonads open into the intestine.

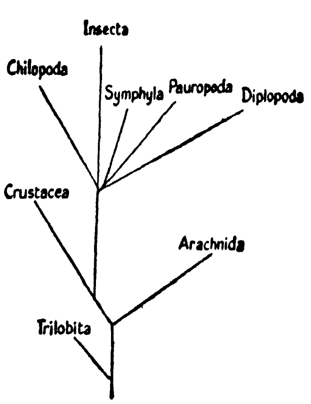
The **Pentastomida** are worm-like and devoid of appendages except two pairs of hooks near the mouth. Their arthropodan affinities are mainly suggested by the larvæ which possess two pairs of clawed, leg-like processes.

The most primitive insects are the bristle-tails or Thysanura, and these lowly creatures exhibit certain structural features which can only be interpreted as inheritances from an ancestral stock. The study of generalized embryos reveals the fact that insects pass through a primordial stage in their development in which the head bears five pairs of appendages and the body is composed of fifteen segments, each bearing a pair of limbs excepting the last. The appendages of the first three body-segments (legs) and of the fourteenth segment (cerci) evidently became more important than the intervening pairs which, for the most part, disappear. It seems clear, therefore, that the ancestors of insects were many-legged animals, and the nearest approach to such progenitors is to be found in the Symphyla, which are, furthermore, related to the Chilopoda and Diplopoda.

The Symphyla exhibit most of the essential structural features required of an ancestor of the Thysanura and, through the latter order, of winged insects. The presence of a Y-shaped epicranial suture and two pairs of maxillæ: of styli and eversible sacs on the abdominal segments: of anal cerci and Malpighian tubes are all characters shared by Symphyla and *Campodea*. The position of the gonopore on the 4th postcephalic segment in Symphyla and on the 11th postcephalic segment in Thysanura seems to be, however, an insuperable difficulty in tracing the actual descent of insects from Symphyla. Their ancestry has to be sought lower down in the arthropod series and probably among a stock which presumably also gave origin to the whole of the myriapods. Theories which derive insects from trilobites or from crustaceans also require mention.

The trilobite theory maintains that the earliest insects were winged forms represented by the extinct Palæodictyoptera which were derived from trilobites, the wings being developed from the pleural expansions so characteristic of the latter group. Traces of such expansions, it is claimed, are also seen in the prothoracic lobes and in the lateral developments of the abdominal segments in these fossil insects. The complete absence of any connecting types bridging the wide gap between trilobites and insects stands in the way of accepting this theory. Also, the assumption that the ancestral type of insect was winged is contrary to accepted opinion.

The crustacean theory maintains that the primitive type of insect was wingless and represented with least modification by the Machilidæ. The theory is largely based upon identity in the number of body segments and structural similarity and homologies of certain of the appendages of *Machilis* and the Syncarida and other Malacostraca. The descent, it is claimed, took place by the crustacean forerunners migrating to the land and there evolving into primitive wingless insects. The relationships between insects and crustaceans, however, are remote and the balance of evidence suggests community of origin rather than the actual derivation of insects from such ancestors.



The hypothetical relationships between insects and other arthropods are expressed in the accompanying diagram and for a discussion of the subject vide Tillyard (1930).

General Organization of an Insect

An examination of the structure and development of the most primitive representatives of the class renders it possible to construct the archetype or ancestral form of winged insect. This hypothetical organism was termed by Paul Mayer the *Protentomon* (Fig. 1) and it is convenient to retain that name although the results of more recent investigation have considerably modified our views with regard to its essential characters. The latter exhibit various secondary modifications in the different orders of insects, but the fundamental or primary features of the *Protentomon* are as follows.

The head is formed by the fusion of six embryonic segments of which the 2nd, and 4th to 6th carry appendages in the adult. These appendages are the antennæ, mandibles, maxillæ and labium (2nd maxillæ). The head also carries a pair of compound eyes and three ocelli.

The thorax consists of three segments each of which bears a pair of legs, and the 2nd and 3rd segments carry a pair of dorso-lateral membranous outgrowths or wings. The two pairs of the latter are similar, and each wing is supported by a system of longitudinal chitinous ribs or veins which are formed around preëxisting tracheæ. There are no true cross-veins but only an irregular network (archedictyon) formed by thickenings of the wing-membrane.

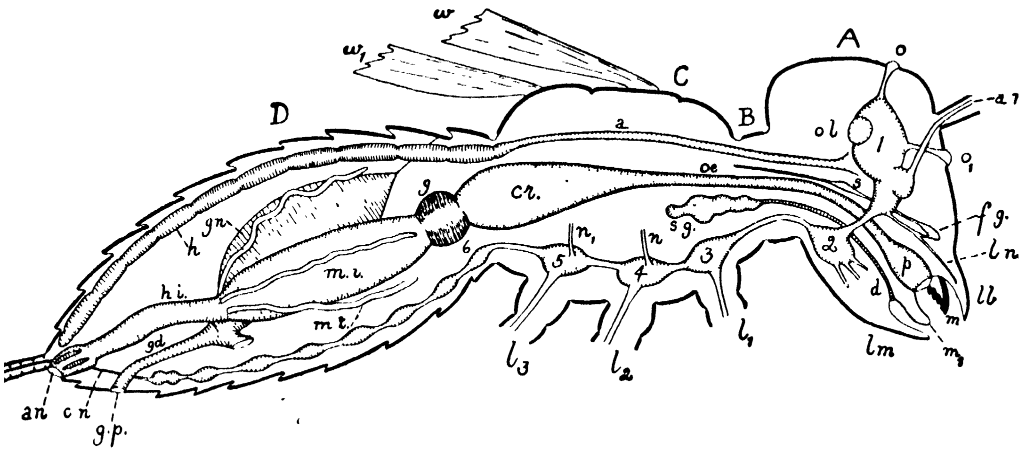


Fig. 1.—The General Organization of a Primitive Winged Insect.

A, head; *B*, cervicum; *C*, thorax; *D*, abdomen; *a*, aorta; *an*, anus; *a.n.*, antennary nerve; *c*, cercus; *c.n.*, nerve to cercus; *cr*, crop; *d*, salivary duct; *f g*, frontal ganglion; *g*, gizzard; *g d.*, gonoduct; *gn*, gonad; *g.p.*, gonopore; *h*, heart; *h.i.*, hind intestine; l_1-l_3, legs; *lb*, labrum; *lm*, labium; *l n*, labral nerve; *m*, mandible; m_1, maxilla; *m.i.*, stomach; *m t*, Malpighian tube; *n*, n_1, alary nerves; o_1, median ocellus; *o*, lateral ocellus; *oe*, œsophagus; *o.l.*, cut end of optic lobe; *p*, pharynx; *s*, œsophageal ganglion; *s g.*, salivary gland; *w*, w_1, wings; 1, brain; 2, sub-œsophageal ganglion; 3–5, thoracic ganglia; 6, 1st abdominal ganglion.

The abdomen consists of eleven segments together with a terminal region or telson: the 11th segment carries a pair of jointed cerci.

The digestive system is divisible into the fore intestine or stomodæum, a simple sac-like stomach or mesenteron and the hind intestine or proctodæum. A pair of salivary glands lie along the sides of the fore intestine, and their ducts pass forwards to unite and form the main salivary duct which opens on the hypopharynx. Six Malpighian tubes are present and arise from the hind intestine near its junction with the mesenteron.

The central nervous system consists of two principal cephalic centres united with a ventral ganglionated nerve cord. The supra-œsophageal centre or brain is formed by the fusion of the three pre-oral cephalic ganglia.

It is joined by means of a pair of para-œsophageal connectives with the sub-œsophageal centre. The latter is formed by the fusion of the three post-oral cephalic ganglia. The ventral nerve cord consists of three thoracic and nine abdominal ganglia united by means of paired connectives. There is consequently one ganglion to each of the first twelve post-cephalic segments.

The dorsal vessel consists of an abdominal portion or heart and a thoracic portion or aorta. The heart is metamerically divided into chambers and each of the latter is provided with paired lateral ostia. Beneath the heart is a transverse septum or pericardial diaphragm. The aorta is a narrow tubular extension arising from the first chamber of the heart and extending forwards through the thorax into the head, where it terminates just behind the brain.

The respiratory system consists of segmentally repeated groups of tracheæ which communicate with the exterior by means of ten pairs of spiracles. These are situated on each of the two hinder thoracic and the first eight abdominal segments respectively.

The genital organs of the two sexes exhibit a very similar morphology. In the male each testis consists of a small number of lobes whose cavities communicate with the vas deferens. The vasa deferentia unite posteriorly and become continuous with a common ejaculatory duct which opens on the ædeagus. Vesiculæ seminales are present as simple dilatations of the vasa deferentia and paired accessory glands open into the proximal portion of the latter. In the female each ovary consists of panoistic ovarioles similar in number to the lobes of the testis. The oviducts combine posteriorly to form a common passage or vagina. A median spermatheca opens on the dorsal wall of the latter, and paired colleterial or accessory glands are also present.

Metamorphosis is of the gradual or hemimetabolous type.

Number and Size of Insects

Insects comprise about 70 per cent. of the known species of all kinds of animals. Approximately 700,000 species of insects have been described, but it is doubtful whether this number represents even one-fifth of those existing to-day. The Coleoptera, with about 250,000 species, form the largest order and among them at least 65,000 species are included in the single family Curculionidæ, while the Chrysomelidæ are not much inferior in point of numbers.

Among living insects, the greatest size is found in individuals of the following species. In the Coleoptera, *Megasoma elephas* attains a length up to 120 mm. and *Macrodontia cervicornis* (including the mandibles) ranges up to 150 mm. Among Orthoptera, *Pharnacia serratipes* may exceed 260 mm. long and the Hemipteron *Belostoma grande* attains a length of 115 mm. For the Lepidoptera their size may, perhaps, be best gauged by the wing-expanse. The latter reaches its maximum in *Erebus agrippina*, whose outspread wings measure up to 280 mm. from tip to tip and in large examples of *Attacus atlas* they measure 240 mm. With regard to the smallest insects certain Coleoptera (fam. Trichopterygidæ) do not exceed a length of ·25 mm. while egg-parasites belonging to the family Mymaridæ are, in some cases, even more minute. As Folsom has observed, some insects are smaller than the largest Protozoa and others are larger than the smallest Vertebrata.

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THE BODY-WALL OR INTEGUMENT

(*a*) Structure

THE body-wall consists of the following layers: (1) the cuticle, (2) the hypodermis, and (3) the basement membrane (Fig. 2).

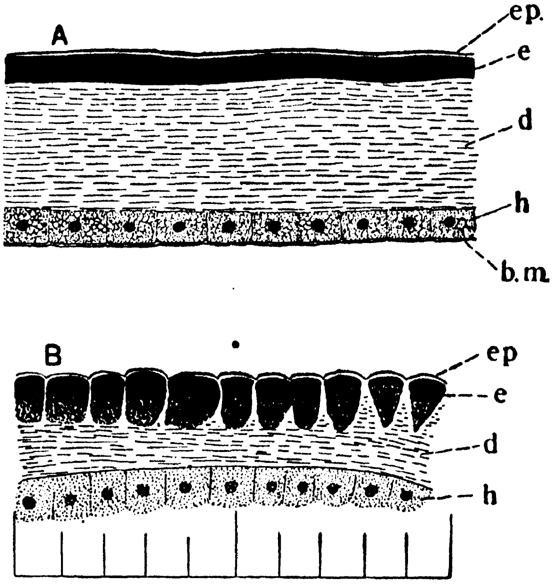

FIG. 2.—STRUCTURE OF THE INTEGUMENT.

A. Diagrammatic section showing structure of insect integument. Original. B. Section through an intersegmental membrane of the larva of *Carabus violaceus*. From Kühnelt (one division of the scale = 0·01 mm.).

ep, epicuticula; *e*, exocuticula; *d*, endocuticula; *h*, hypodermis; *b.m*, basement membrane.

The **Cuticle** (cuticula) is the outermost investment of the body and appendages and is largely composed of the substance known as *chitin*. When newly formed it is flexible and elastic and it remains in this condition as the intersegmental membranes, the articular membranes of the appendages and in other situations. For the most part, however, the cuticle forms a hard inelastic exoskeleton which is due to its subsequently undergoing certain chemical changes. The nature of the change is not known, and among many insect larvæ the cuticle remains membranous and apparently unaltered. Two distinct layers of the cuticle are evident in most insects,—the *exocuticula* or epidermis and the *endocuticula* or dermis. The exocuticula is the hard, outer, homogeneous layer which is the seat of the cuticular pigments: setæ of various types and the cuticular parts of sense organs derived from them, are mostly formed from this layer. The endocuticula is the inner, more flexible and usually much thicker layer which exhibits a laminated structure. The intersegmental membranes owe their flexibility either to the absence of the exocuticula from such areas or, more usually, to the thinness of the exocuticula or to its discontinuous structure (Fig. 2). In most insects a very thin stratum or *epicuticula* (less than 1 μ in thickness) is present outside the exocuticula. According to Kühnelt (1928) it does not contain chitin and is allied chemically to plant cuticle. Minute pore-canals pass through the cuticle in various regions of the body, and connect with the cavities of the cuticular appendages, or allow of the passage of the secretion of dermal glands. There are also numerous other pore-canals unconnected with either of these functions. These are often difficult to detect and do not penetrate the epicuticula to open to the exterior : they are stated to be occupied by fine protoplasmic processes of the cells of the hypodermis (Fig. 3). The cuticle may be smooth and glistening or variously punctured, granulated, striated or otherwise sculptured. In surface view it sometimes exhibits a division into small polygonal areas which form an irregular reticulated pattern.

Chitin is an essential constituent of the exoskeleton of arthropods, but it is by no means confined to that phylum. It has been found in representatives of many classes of invertebrates and also enters into the composition of the cell-wall of fungi. Among insects, in addition to being deposited externally, it also occurs internally and, in special, wherever organs or parts are developed as invaginations of the integument. Thus, the endoskeleton is a cuticular product, as are also the linings of the stomodæum and proctodæum, of the tracheæ, of the ducts of the salivary and other glands and the main genital passages : the peritrophic membrane is also chitinous. Whether chitin is a regular constituent of the lining of the smaller tracheæ and the air sacs of insects is, however, uncertain.

Pure chitin is colourless and insoluble in water, alcohol, in dilute or concentrated alkalies or in dilute acids. It may be boiled in concentrated alkali for long periods without change of appearance, but becomes hydrolyzed to form chitosan and acetic acid. At room temperature it is oxidized and dissolved in a solution of sodium hypochlorite if the latter contains 5 per cent. available chlorine (Campbell). Chitin is hydrolyzed and dissolved by concentrated mineral acids.

Chemically chitin is a nitrogenous polysaccharide whose exact empirical formula is uncertain : according to Brach (1912) it is probably $(C_{32}H_{54}O_{21}N_4)x$. Its specific gravity is near 1·398 (Sollas) and its refractive index is 1·525 ± ·005 (Becking and Chamberlain). It is doubtful whether chitin often occurs without admixture with other substances of unknown composition. According to Campbell (1929) the hardness of insect cuticle is due to the presence of such substances and is, consequently, not indicative of the amount of chitin present.

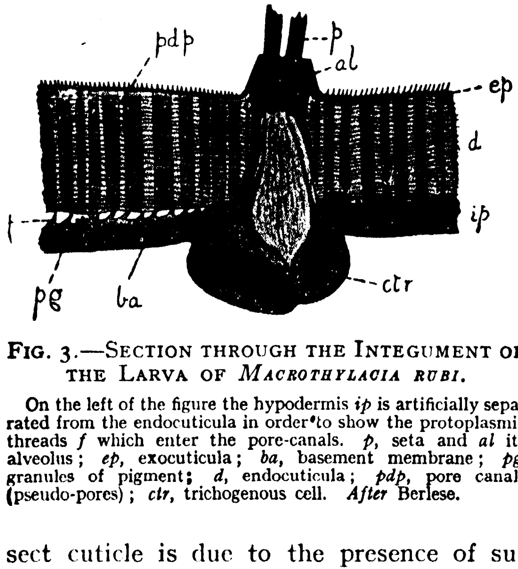

FIG. 3.—SECTION THROUGH THE INTEGUMENT OF THE LARVA OF *MACROTHYLACIA RUBI.*

On the left of the figure the hypodermis *ip* is artificially separated from the endocuticula in order to show the protoplasmic threads *f* which enter the pore-canals. *p*, seta and *al* its alveolus ; *ep*, exocuticula ; *ba*, basement membrane ; *pg*, granules of pigment ; *d*, endocuticula ; *pdp*, pore canals (pseudo-pores) ; *ctr*, trichogenous cell. *After* Berlese.

It is generally recognized that the most satisfactory test for chitin involves its conversion into chitosan. The material, after being freed of tissue, etc., is placed in a solution of potassium hydroxide, saturated at room temperature, and heated in an oil bath kept at 160° C. for 15 minutes. After cooling the material is best freed from alkali by passing through grades of alcohol of descending strength before being washed in water. It is now ready to be tested, and if the sample has been converted into chitosan it becomes coloured violet when treated with 0·2 per cent. iodine (in potassium iodide solution) in 1 per cent. sulphuric acid. Chitosan, furthermore, will dissolve in 3 per cent. acetic acid, whereas unaltered chitin is insoluble. The addition of a drop of 1 per cent. sulphuric acid results in the formation of a white precipitate (chitosan sulphate). Further information on chitin will be found in papers by Wester (1910), Kühnelt (1928), Campbell (1929), and Yonge (1932).

The **Hypodermis** forms a continuous layer of cells. The latter are usually flattened or somewhat columnar, and the cell boundaries are often hard to detect and frequently only visible in tangential sections. The hypodermal cells often contain pigment and function in secreting the cuticle.

The **Basement Membrane** is a continuous apparently structureless layer bounding the inner surface of the hypodermis. It is extremely thin and often difficult to detect and, according to Mayer, it is composed of nucleated stellate cells with the interstices filled in with a homogeneous intercellular substance.

(*b*) Cuticular Appendages

These structures include all outgrowths of the cuticle that are connected with it by means of a membranous joint. They may be classified into setæ and spurs.

Setæ or **Macrotrichia** (Fig. 3) are commonly known as hairs and each arises from a cup-like pit or *alveolus* situated at the outlet of a pore-canal. At its base the seta is attached by means of a ring of articular membrane. Setæ are hollow structures developed as extensions of the exocuticula and each is produced by a single, usually enlarged, hypodermal cell or *trichogen*. The articular membrane is usually produced by a second hypodermal cell or membrane cell. In recent years *chætotaxy*, or the study of the arrangement of the more important setæ, has assumed a good deal of significance from the taxonomic point of view, particularly with reference to the Cyclorrhapha and larval Lepidoptera. The following are the principal types of setæ commonly met with :—(1) *Clothing hairs*.—These invest the general surface of the body or its appendages and frequently exhibit various degrees of specialization. When furnished with thread-like branches as in the Apidæ they are termed *plumose hairs*. Setæ which are particularly stout and rigid are known as *bristles*, which are well exhibited for example in the Tachinidæ. (2) *Scales*.—These structures are highly modified clothing hairs and are characteristic of all Lepidoptera and many Collembola : they are also present in certain Diptera and Coleoptera. Transitional forms between ordinary clothing hairs and scales are frequent. (3) *Glandular setæ*.—Grouped under this heading are those setæ which function as the outlet for the secretion of hypodermal glands (vide p. 148). If they are especially stout and rigid they are then termed *glandular bristles* as in the urticating hairs of certain lepidopterous larvæ. (4) *Sensory Setæ*.—Very frequently the setæ of certain parts of the body, or more particularly the appendages, are modified in special ways and become sensory in function. Sensory setæ (vide p. 71) are in all cases connected with the nervous system.

Spurs occur on the legs of many insects and differ from setæ in being of multicellular origin (Comstock).

(*c*) Cuticular Processes

The external surface of the cuticle, in addition to being sculptured in various ways, bears a great variety of outgrowths which are integral parts of its substance. They are rigidly connected with the cuticle, having no membranous articulation and, in the absence of the latter feature, they are readily separable from cuticular appendages. The principal types of cuticular processes are as follows.

Microtrichia (fixed hairs or aculei).—These are minute hair-like structures found, for example, on the wings of the Mecoptera and certain Diptera. They resemble very small covering hairs, but the absence of the basal articulation is their distinguishing feature (Figs. 3 and 26).

Spines.—This expression has been used by various writers with considerable latitude and, in the present work, it is confined to outgrowths of the cuticle which are more or less thorn-like in form. According to Comstock spines differ from spine-like setæ in being produced by undifferentiated hypodermal cells and are usually, if not always, of multicellular origin.

In addition to the above there is also a great variety of other cuticular processes which either take the form of more or less conical *nodules* and *tubercles* of different shapes, or of larger projections known as *horns* which are a characteristic feature in the males of certain Coleoptera.

(*d*) Coloration

The colours of adult and immature insects may be grouped into three classes: (1) pigmentary or chemical colours, (2) structural or physical colours, and (3) combination or chemico-physical colours.

1. Pigmentary Colours.—These owe their presence to substances of definite chemical composition which have the property of absorbing some light waves and of reflecting others. Such substances are for the most part products of metabolism and in some cases are known to be of an excretory nature. They may be classified into cuticular, hypodermal and subhypodermal colours according to their location. Frequently a colour pattern consists of a ground colour whose source lies in the hypodermis or underlying tissues, and is overlaid by blotches of a cuticular pigment.

Cuticular colours are mostly contained in the exocuticula: they consist of browns, blacks and yellows, which are permanent.

Hypodermal colours are lodged in the form of granules or drops of fat in the cells of the hypodermis. They may be red, orange, yellow or green and are very evanescent after death.

Subhypodermal colours are contained in the fat-body and blood.

The more important insect pigments may be grouped into four categories.

(1) *Chlorophyll and other derived Pigments.*—In this group are included pigments of vegetable origin which are absorbed from the food and apparently undergo little or no change in composition in the process. They comprise chlorophyll and its components, anthocyanins and flavones.

The early researches of Poulton (1894) indicated that a modified chlorophyll occurs in the blood and integument of lepidopterous larvæ and forms the prevailing green coloration of many species. Carotin, the orange-yellow component of chlorophyll, is known to produce the yellow or red coloration in Coccinellidæ and Chrysolelidæ among Coleoptera and in Pyrrhocoridæ and Pentatomidæ among Hemiptera. The work of Palmer and Knight (1924) and Knight (1924) indicates that the red and yellow coloration of *Perillus bioculatus*, a member of the last-mentioned family, is largely due to carotin absorbed from the tissues of its prey (*Leptinotarsa*). The latter, in its turn, is coloured deep orange by carotin derived from its food plant (the potato). Whether a yellow pigment present among lepidopterous larvæ is due to xanthophyll or carotin appears to be uncertain. Anthocyanin pigments are stated to be present in the larvæ of the beetle *Cionus olens* and in certain aphides. A yellowish pigment of the nature of a flavone is present in the wings of the butterfly *Melanargia galatea* and a similar pigment occurs in its food plant (Thompson, 1926). Palmer and Knight (1924A) record the occurrence of flavones in certain families of Hemiptera-Heteroptera.

(2) *Hæmoglobin and allied Pigments.*—Hæmoglobin is of rare occurrence among insects. In certain Chironomid larvæ it is present in the blood plasma and, since they possess a transparent integument, imparts to them their characteristic red appearance. Hæmoglobin also occurs under localized conditions in a few other insects (p. 130), but plays no part in coloration. The red and yellowish pigments present in the wing scales of *Vanessa* butterflies are stated by Grafin von Linden (1905) to present certain affinities with hæmoglobin.

(3) *Pigments of Protein Origin.*—These include the melanin group of pigments produced by the oxidation of an animo-acid (tyrosin) through the action of an enzyme (tyrosinase). Darkened or black forms of many insects, especially Lepidoptera, are often termed " melanics " without evidence that melanin is the pigment involved. The chromogen tyrosin has been found in various insects, and it is probable that melanin is a widely spread pigment among these animals. Its actual occurrence

has been determined in a few cases, notably by Onslow (1916) with reference to the black markings of the wings of *Pieris brassicæ*, and by Gortner (1911) in Coleoptera. Hasebroek and others state that in many insects the chromogen involved is dopa (dioxyphenylaline) which becomes converted into melanin by a dopaoxidase, but biochemical knowledge of this difficult subject is very restricted.

(4) *Pigments with Purine Bases.*—Uric acid and its derivatives are the end products of purine metabolism in insects. Normally most of such substances are voided through the alimentary canal but, among the Pieridæ, a certain amount becomes deposited in the wing scales, giving rise to the white, red and yellow colours of those insects (Hopkins 1896, Wigglesworth 1924). Excretory substances of this nature are not known to function as pigments in any other family of Lepidoptera. More recently Mason (1926) has stated that the white colour in Pieridæ is a structural property of the scales themselves since it remains after extraction of the uric acid.

2. Structural Colours.—The beautiful iridescent colours of many insects are extremely difficult to account for and various theories have been advanced to explain them. Such colours prevail not only in wings devoid of pigment but also remain in pigmented parts after bleaching. Immersion in liquids of appropriate refractive index destroys iridescent colours, but they are restored after washing and drying. Recent investigators regard interference of light at the surfaces of single or multiple films as accounting for the largest number of examples of iridescent colours. These films are represented by extremely delicate laminæ which, according to Mason, may be located in the striæ of the wing scales (*Morpho*), in the scale wall (*Urania*) or in the interior of the scale (*Entimus*). Diffraction of light, as at the surface of a grooved structure or "grating," is apparently seldom involved: the powdery "bloom" or efflorescence present on the body and wings in some Odonata is regarded by Mason as owing its bluish colour to the scattering of light by the minute particles concerned. White is usually produced by reflection or refraction of light by structural elements located in the scales or other cuticular parts.

3. Combination Colours.—These are produced by a structural modification in conjunction with a layer of pigment and are much commoner than purely structural colours. In the butterfly *Teracolus phlegyas* a red pigment in the scale wall (but not in the striæ) combines with a structural violet to produce magenta: in *Ornithoptera poseidon* the emerald green is due to a structural blue combined with a yellow pigment in the walls and striæ of the scales. In a number of cases (e.g. Lycænids) there is no indication of the cause of colour. The golden iridescence of *Cassida* and its allies is produced by a film of moisture beneath the surface cuticle. These insects rapidly lose their colour when dried, but it returns after soaking in water provided the drying has not been too prolonged.

(*e*) Literature on the Body Wall and Coloration

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Coloration.

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SEGMENTATION AND THE DIVISIONS OF THE BODY

THE cuticle of an insect forms a more or less hardened exoskeleton and, although perfectly continuous over the whole body, it remains flexible along certain definite and usually transverse lines. In the latter positions the cuticle becomes infolded and is membranous in character. The body of an insect consequently presents a jointed structure which is termed *segmentation*, and is divided into a series of successive rings variously known as *segments*, *somites*, or *metameres*. The flexible infolded portion of the cuticle between adjacent segments is the *intersegmental membrane* whose function is to allow of the freedom of movement of the body.

It must be borne in mind that segmentation is not only manifested in the external differentiation of the body but it involves most of the internal organs also. In the Annelida and the Onychophora the internal structure of an individual segment is very similar to that of the segment preceding or following it. This is due to the fact that there is a repetition of the organs or parts through most of the segments of the body. In such highly evolved animals as insects the primitive segmentation, in so far as it affects the internal anatomy, has undergone profound modifications; the segmental repetition of parts is nevertheless to a large extent retained in the central nervous system, the heart, tracheal system and in the body musculature.

The cuticle also exhibits localized areas of hardening termed *sclerites* which meet one another along certain lines of union known as *sutures*. In the case of movable sclerites their membranous continuity may be concealed but, if the cuticle of an insect be distended, many of the sclerites will be forced apart, and it is then seen that they are connected by membrane, along the lines of the sutures. Others of the sclerites are rigidly fixed and cannot be separated in this manner, the sutures in these cases being little more than linear impressions. In certain regions the sclerites do not come into apposition by sutures and are thus, as it were, islands of cuticle surrounded by membrane. Complete fusion of adjacent sclerites is common, particularly among the higher orders of insects, all traces of sutures being lost.

(*a*) The Divisions of a Body-Segment

In the majority of adult insects, and in many of their larvæ, the body-wall of a typical segment is divisible into four definite sclerotized regions. A dorsal region or *tergum*, a ventral region or *sternum*, and a lateral region or *pleuron* on each side of the body. Each of these regions may be differentiated into separate sclerites. In this case the sclerites composing the tergum are known as *tergites*, those of the sternum as *sternites*, and those constituting each pleuron as *pleurites*. Between adjacent segments there may be present small detached plates or *intersegmentalia* and such sclerites belong partly to the segment in front and partly to the segment behind them. According to their position they are termed *intertergites, interpleurites* and *intersternites.*

(*b*) The Appendages

In the embryo each body segment may bear a pair of outgrowths or appendages which may, or may not, be retained in post-embryonic life. Among adult insects, an appendage is normally attached to its segment between the pleuron of its side and the sternum. Typical appendages are jointed tubes invested with a dense cuticle. Between each pair of joints, or segments, the cuticle remains membranous and becomes infolded to form the articular membrane. On account of its jointed structure, the whole or part of an appendage is movable by means of its muscles. An insect appendage consists typically of a limb base and a shaft which represents the endopodite of Crustacea. There is no conclusive evidence of a biramous condition among the appendages in any insects.

(*c*) Processes of the Body-Wall

In addition to true appendages numerous other outgrowths of the body wall are found in various insects. Unlike true appendages, processes of the body-wall are by no means invariably represented by embryonic counterparts ; they may or may not be segmentally arranged, they may be originally paired or unpaired, and more than a single pair is sometimes borne on a segment. They differ from cuticular processes in containing a definite extension of the body cavity and in some cases they are freely movable. The principal types of organs which come under this category are :—(1) *Pseudopods,* which are characteristic of many dipterous larvæ. (2) *Scoli,* or thorny processes, characteristic of Nymphalid and Saturniid larvæ : the anal horn of Sphingid larvæ is also of a very similar nature. (3) *Branchiæ* or gills which are found in most larvæ of aquatic insects (vide p. 124). (4) *Wings* (vide p. 32), which are always confined to the meso- and metathorax and attain their full development in adult insects.

(*d*) The Regions of the Body

The body segments of an insect are grouped together to form three usually well defined regions—the *head,* the *thorax* and the *abdomen* (Fig. 1). In each of these regions certain of the primary functions of the organism are concentrated. The head carries the mouth-parts, which are concerned with feeding, and the organs of special sense. The thorax bears the locomotory organs, e.g., legs and wings. The abdomen is concerned with reproduction and may carry appendages associated with the latter function ; it is also the seat of the metabolic processes of the body.

In most orders an intersegmental region or *cervicum* connects the head with the thorax.

of Isoptera, by a backward extension of the postmentum and genæ. Or, as among Coleoptera, a median ventral sclerite or *gula* extends from the occipital foramen to the base of the submentum. It occupies the area between the postoccipital sutures which, along with the posterior tentorial pits, have extended forwards on the head capsule. Where these sutures bound the gula laterally they are often termed *gular sutures*. In most cases the gula and submentum are fused into a single plate (Fig. 11) which may be termed the *gulamentum*.

In addition to the foregoing there are other sclerites of lesser importance which although not of general occurrence, are nevertheless present in certain insects or their larvæ. These are—(1) The *antennal sclerites* (Fig. 4). Each is a ring of chitin into which the basal joint of the antennæ of its side is inserted. (2) The *ocular sclerites*. These are similarly annular in form and each surrounds the compound eye of its side. (3) *The mandibular sclerite*. A small sclerite close to the base of the mandible and separated by a transverse suture from the gena: it is found in many Orthoptera (Figs. 4 and 5).

(*b*) The Antennæ

These are a pair of very mobile jointed appendages which are articulated with the head in front of or between the eyes. In the more generalized insects the antennæ are filiform and many-jointed, the joints being equal or sub-equal in size. They vary, however, very greatly in form in the higher

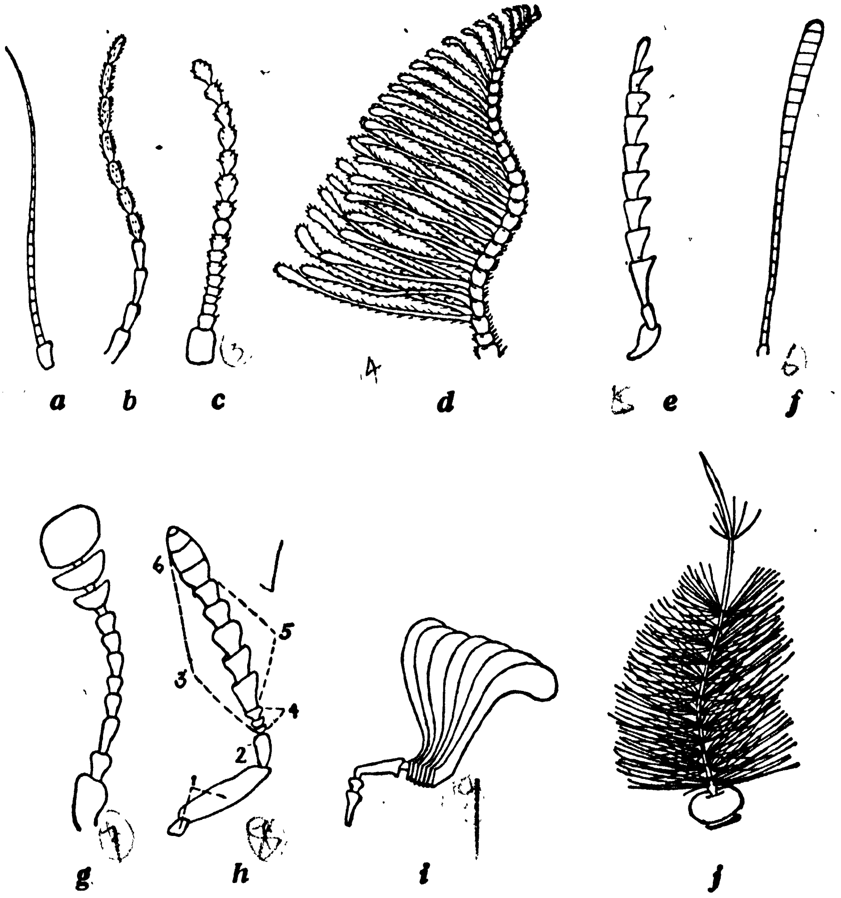

FIG. 7.—TYPES OF ANTENNÆ.

a, setaceous (*Blatta*); *b*, filiform (*Carabus*); *c*, moniliform (*Calotermes*); *d*, pectinate (Tenthredinid, after Enslin); *e*, serrate (Elaterid); *f*, clavate (Lepidopteron); *g*, capitate (*Necrobia*); *h*, geniculate (Chalcid); *i*, lamellate (*Melolontha*, after Newport); *j*, plumose (male of *Culex*); 1, scape; 2, pedicel; 3, flagellum; 4, ring-joints; 5, funicle; 6, club.

orders and certain of the joints are frequently differentiated from their fellows. In the more specialized insects the antenna is divisible into scape, pedicel and flagellum (Fig. 7).

The *scape* is the first or basal joint of the antenna and is often conspicuously longer than any of the succeeding joints.

The *pedicel* is the joint which immediately follows the scape. It is present in geniculate antennæ where it forms the pivot between the scape and flagellum.

The *flagellum* (or *clavola*) forms the remainder of the antenna. It varies greatly in form among different families in adaptation to the particular surroundings and habits of the species concerned. In some insects, particularly among Hymenoptera, the flagellum is divisible into the ring-joints, the funicle and the club. The ring-joints are commonly present among the Chalcidoidea, where the basal joint or joints of the flagellum are of much smaller calibre than the joints that follow, and are ring-like in form. In these instances the name of ring-joints has been applied to them. The *club* is formed by the swollen or enlarged distal joints of the antenna. The *funicle* comprises those joints which intervene between the ring-joints and the club, or between the latter and the pedicel in cases when the ring-joints are not differentiated.

The antennæ afford important secondary sexual characters which are particularly well exhibited in the pectinated or bipectinated organs of certain male Lepidoptera, and in the densely plumose antennæ of male Culicidæ and Chironomidæ. Functionally the antennæ are organs of special sense (vide p. 74) but in a few exceptional cases they are modified for other uses. Thus in the larvæ of *Chaoborus* and its allies they are adapted for seizing the prey, while those of the male of *Melöe* are used for holding the females. In larvæ of the Hymenoptera Apocrita and the higher Diptera the antennæ are often reduced to minute tubercles or are atrophied. They are wanting in all Protura.

(*c*) The Mouth-parts or Trophi

These organs consist typically of the *labrum* or upper lip, the *labium* or lower lip, an anterior or upper pair of jaws termed the *mandibles* and a posterior or lower pair of jaws termed the *maxillæ*. Arising from the floor of the mouth, is a median tongue-like structure or *hypopharynx*, and associated with the latter in the more primitive orders are small paired lobes or *superlinguæ*. The mouth-parts vary in form to a greater degree than almost any other organs, the variation being correlated with the method of feeding and other uses to which they may be subjected. An examination of the structure of the mouth-parts, therefore, will give a clue to the method of feeding and frequently to the nature of the food of an insect. The various modifications which these organs undergo are of fundamental importance for purposes of classification and are dealt with in the chapters devoted to the different orders of insects.) Most of the latter fall into two classes, viz., those with mandibulate or biting mouth-parts and those with suctorial or haustellate mouth-parts. Both these functions are combined in most Collembola and in the Hymenoptera : in the Hemiptera, Thysanoptera and certain of the Diptera the mouth-parts are adapted for piercing the tissues of plants or animals. In the Ephemeroptera, and certain Lepidoptera and Diptera these organs are greatly reduced or non-functional.

The *labrum* (Fig. 4) is a simple plate hinged to the clypeus and capable of a limited amount of up and down movement. It overlies the bases of the mandibles and forms the roof of the buccal cavity. Morphologically it represents the most anterior region of the head and has secondarily acquired a basal hinged attachment. Its ventral or pharyngeal surface is usually provided with gustatory organs and forms the *epipharynx* or membranous roof of the mouth. In many insects the epipharynx is produced in the form of a median fold which is more or less sclerotized. Among Diptera it is intimately associated with the elongated labrum and the whole organ is termed the *labrum-epipharynx.*

The *mandibles* (Fig. 8) or true jaws each represent the basal joint or coxopodite of the typical Arthropod limb. They are adapted for cutting or crushing the food and frequently also for defence : more rarely they are modified into either sickle-like or stylet-like piercing organs. In the soldiers of the Isoptera they assume grotesque and inexplicable forms and in certain Coleoptera (*Lucanus, Chiasognathus,* etc.) they exhibit dimorphism, attaining relatively enormous proportions in the male. Typically, the mandible is a solid compact piece articulating with the head by means of a *ginglymus* and *condyle.* The former is a groove or cavity which articulates with a convex process of the clypeus and the condyle is a rounded head adapted to fit into a socket placed at the lower end of the gena or postgena. Each jaw is moved by means of powerful adductor and abductor muscles. In phytophagous insects the mandibles are bluntly toothed and often bear a molar or crushing surface near the base of the biting margin. In carnivorous forms the teeth are sharply pointed, being adapted for seizing and cutting, and the molar surface is wanting. In certain insects the mandibles exhibit more or less evident indications of a secondary division into separate sclerites. In the Machilidæ (Fig. 9) for example, they are segmented into a proximal and distal piece, and traces of several sclerites are found in *Cetonia, Copris* and other Coleoptera. In some cases a flexible plate or *prostheca,* fringed with hairs, is present on the inner border of the mandible and has been incorrectly homologized with a lacinia. Mandibles are wanting in many adult Trichoptera and the vast majority of Diptera, and they are absent or vestigial in almost all Lepidoptera.

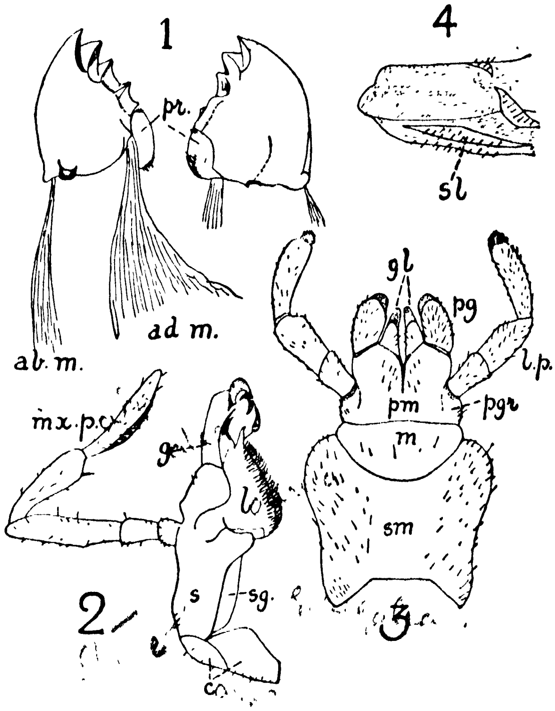

FIG. 8.—MOUTH-PARTS OF *BLATTA.*

1, Mandibles. *ab.m,* abductor muscle; *ad.m,* adductor muscle; *pr.,* prostheca ; 2, Maxilla—*c cardo;* *g,* galea; *l,* lacinia; *mx.p,* maxillary palp; *s,* stipes; *sg,* subgalea; 3, Labium—*gl,* glossa; *l p,* labial palp; *m,* mentum; *pg,* paraglossa; *pgr,* palpiger; *pm,* prementum; *sm,* submentum; 4, Hypopharynx—*sl,* rudiment of left superlingua.

The *maxillæ* (Figs. 8–10) are composed of the following sclerites. The *cardo* or hinge is the first or proximal piece and, in many insects, is the only portion directly attached to the head. The *stipes* or footstalk articulates with the distal border of the cardo and bears a lateral (outer) sclerite or *palpifer* and sometimes an inner sclerite, the *subgalea* (or *parastipes*). The palpifer carries the *maxillary palpus* which is the most conspicuous appendage of the maxillæ. It is one to seven-jointed and sensory in function. In many insects the subgalea is not evident as a separate sclerite, being either fused with the lacinia or merged into the stipes. Distally the maxilla is composed of two lobes : an outer one or *galea* and an inner one or *lacinia.* The former is often two-jointed and frequently partially overlaps the lacinia after the manner of a hood. The lacinia or blade as a rule is spined or toothed on its inner border and, in cases when it is fused with the subgalea, it has the appearance of carrying the galea. In certain cases (e.g. many coleopterous larvæ) each maxilla carries a single lobe or *mala* which is possibly homologous with the galea, the lacinia being undeveloped. Functionally the maxillæ are a pair of accessory jaws, their laciniæ aiding the mandibles in holding the food when the latter are extended, as well as assisting in mastication. In many of the higher insects the maxillæ are so greatly modified that they no longer retain any evidences of their primitive structure. In piercing insects they are styliform and their palpi atrophied.

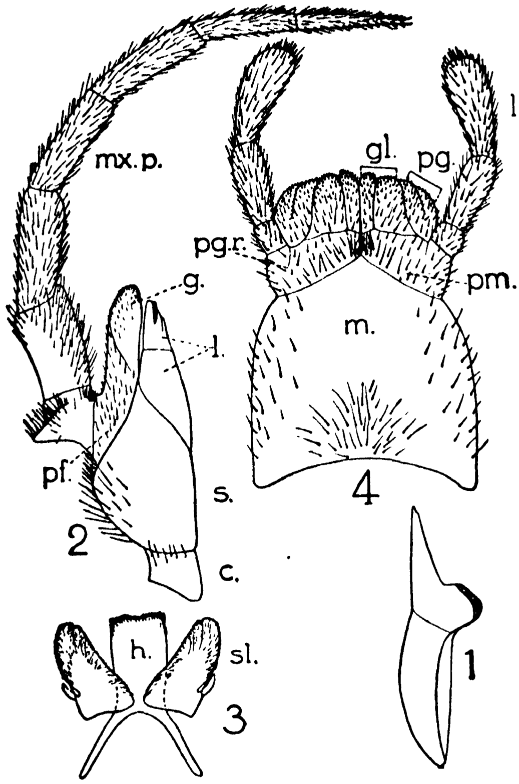

FIG. 9.—MOUTH-PARTS OF *PETROBIUS MARITIMUS.*

1, Mandible. 2, Maxilla. *pf*, palpifer. 3, Hypopharynx (*h*) and superlinguæ (*sl*). 4, Labium. *m*, postmentum. Other lettering as in Fig. 8.

The insect maxilla is to be regarded as the highly modified derivative of a walking limb, whose main shaft is represented by the palpus and base by the cardo and stipes. Hansen, and also Crampton, claim that a reduced third element, the palpifer, enters into the formation of the limb base. On this interpretation the galea and lacinia are masticatory lobes, or endites, of the palpifer and stipes respectively. Börner and Snodgrass regard the palpifer as a secondarily demarcated portion of the stipes and of little morphological importance. On Snodgrass' theory the galea and lacinia are subdivisions of a single endite of the stipes.

The *superlinguæ* (often termed maxillulæ) are a pair of dorso-lateral lobes attached to the hypopharynx (Fig. 9). They are best developed among Thysanura where they appear strikingly like a pair of reduced jaws : in the Machilidæ each is distally cleft and bears an outer, one-jointed, palp-like appendage. Superlinguæ are also well-developed in the Collembola and nymphs of the Ephemeroptera, besides being present in a more or less reduced condition in other mandibulate orders, and in some larvæ (vide Evans, 1921). Hansen (1893) and several morphologists after him, have homologized the superlinguæ with the Crustacean maxillulæ, hence regarding them as true appendages. Crampton (1921), on the other hand, states that they are homologous with the paragnaths of Crustacea, which have similar relations with the hypopharynx in those animals. The term maxillulæ, therefore, is undesirable since it implies an homology which is unproven.

The *labium* (or second maxillæ) (Figs. 8, 9, 11, 12, 13) is formed by the fusion of a pair of appendages serially homologous with the maxillæ. The completeness of the fusion that has taken place varies greatly in different orders of insects, and evidences of the original paired condition are clearly seen among the lower orders. The labium is divided into two primary regions—a proximal *postmentum* and a distal *prementum*, the line of division between the two being the *labial suture*. The muscles of the palpi and the terminal lobes originate within the body of the prementum and consequently lie anterior to the labial suture. The median retractor muscles of the prementum, on the other hand, arise in the postmentum and have their insertions on the proximal margin of the prementum (Fig. 13). The relationships of these muscles, therefore, aid in determining the homologies of the main parts of the labium. The postmentum remains as an undivided plate in, for example, the Thysanura and Isoptera. In many Orthoptera a distal sclerite or *mentum* is developed immediately behind the labial suture and the proximal area of the original postmental plate is termed the *submentum*. The mentum is frequently ill-defined and is without muscle attachments: in the higher orders it appears to have atrophied and in such cases the single basilabial plate is the submentum. Near the base of the prementum, on either side, is the *palpiger* which carries the *labial palpus* and often resembles a basal joint of the latter. The labial palpi are composed of from one to four joints and they function as sensory organs. Arising from the distal margin of the prementum are two pairs of lobes which collectively form the *ligula*, viz.:—an outer pair or *paraglossæ*, and an inner pair or

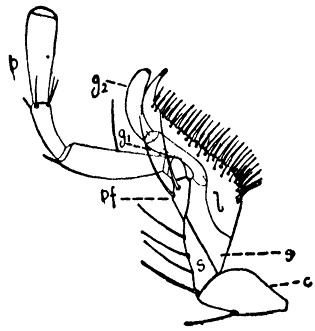

FIG. 10.—RIGHT MAXILLA (VENTRAL ASPECT) OF A BEETLE, *NEBRIA BREVICOLLIS*.

c, cardo; g_1, g_2, proximal and distal points of galea; *l*, lacinia; *p*, palp; *pf*, palpifer; *s*, *s*, stipes.

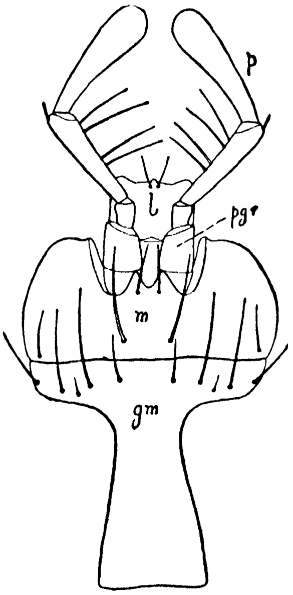

FIG. 11.—LABIUM (VENTRAL ASPECT) OF *NEBRIA BREVICOLLIS*.

gm, gulamentum; *l*, ligula; *m*, mentum; *p*, palp; *pgr*, palpiger.

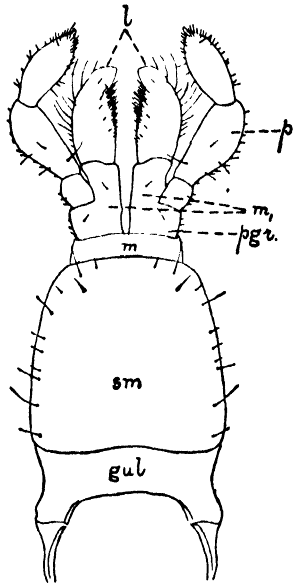

FIG. 12.—LABIUM OF *FORFICULA* (VENTRAL ASPECT).

l, ligula; *gul*, gula; *m*, mentum; *p*, palp; *pgr*, palpiger; m_1, prementum; *sm*, submentum.

glossæ. More usually, the latter organs are fused to form a median *glossa* or the prementum may bear a single median lobe to which the general term ligula is applied.

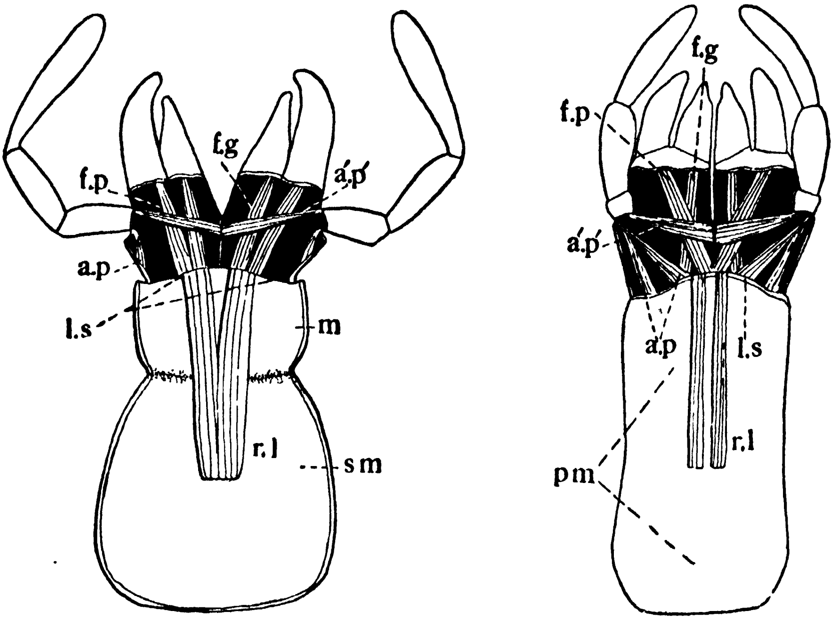

FIG. 13.—RIGHT, LABIUM OF *GRYLLOBLATTA* (adapted from Walker). LEFT, LABIUM OF *MASTOTERMES* (original). In both figures the wall of the prementum has been removed to show the musculature.

a.p, abductor of palp ; *a'.p'*, adductor of palp ; *f.g*, flexor of glossa ; *f.p*, flexor of paraglossa ; *l.s*, labial suture ; mentum ; *p.m*, postmentum ; *r.l*, median retractors of prementum ; *sm*, submentum.

In Fig. 14 the homologies of the sclerites of the labium with those of the maxillæ are indicated. The glossæ and paraglossæ are the counterparts of the laciniæ and galeæ respectively, while the labial palpi are homologous with similar organs of the maxillæ. The two lobes of the primitive divided prementum are clearly traceable as the representatives of the stipites which, in most insects, undergo fusion. The only part comparable to united cardines is the postmentum, but it is possible that the median part of the sternum of the labial segment is incorporated in this sclerite. The true morphological explanation of the postmentum is unsolved and further embryological data are needed. The mentum has frequently been homologyzed with the stipites, but since the former sclerite is a secondary development it is of little morphological importance and the homology referred to is untenable.

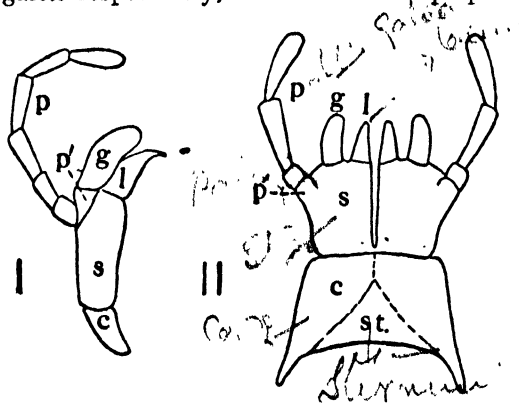

FIG. 14.—DIAGRAM SHOWING HOMOLOGOUS PARTS IN MAXILLA (I) AND LABIUM (II).

c, cardo ; *s*, stipes ; *l*, lacinia ; *g*, galea ; *p*, palp ; *p'*, palpifer (or palpiger in II) ; *st*, sternum.

The *hypopharynx* (or *lingua*) (Fig. 9) is a median tongue-like process arising from the floor of the mouth-cavity, and bearing the aperture of the common salivary duct. The superlinguæ are always closely associated with the hypopharynx and, in many cases, their vestiges are fused with it on either side. In the Diptera the hypopharynx is either awl-like or stylet-like, and in some cases it is used as a piercing organ.

(*d*) Segmentation of the Head

After an insect has emerged from the egg the completed head exhibits but few clear indications of its segmental origin apart from the fact that it carries paired appendages. As long ago as 1816 Savigny concluded that the movable appendages of the head were serially homologous with legs. As each segment only bears a single pair of appendages it was evident that at least four segments enter into the composition of the head, i.e., the antennary, the mandibular, the maxillary and the labial. Huxley in 1878 recognized these four segments and pointed out that the crustacean second antennæ were wanting in insects but, if their segment be presumed to be retained though without bearing appendages, and the eyes be taken to represent the appendages of another segment, the insect-head is composed of six segments. Janet (1899), from a study of ants, considered that nine segments enter into the composition of the head, but his results have not been accepted. It may be said, therefore, that Huxley's conclusions were the most satisfactory that could be derived solely by means of comparative morphology. The foundation of modern knowledge of the segmentation of the head is mainly embryological and is due to Viallanes, Wheeler, Uzel, Heymons, Wiesmann and other workers. The results of their researches have been to establish definitely the existence of six cephalic segments in all insects. Embryology affords three fundamental characters which provide the strongest evidence with reference to segmentation, viz., the existence of paired appendages, of neuromeres and of primitive cœlom sacs. On the basis of these three criteria the segments which enter into the composition of the insect head may be shown in tabular form as below :—

Segment.	*Neuromere.*	*Cœlom Sacs.*	*Appendages.*
1. Ocular . .	Protocerebrum	Present	Embryonic
2. Antennal . .	Deutocerebrum	do.	Antennæ
3. Intercalary .	Tritocerebrum	do.	Embryonic
4. Mandibular .	Mandibular ganglion	do.	Mandibles
5. Maxillary . .	Maxillary ganglion	do.	Maxillæ
6. Labial . .	Labial ganglion	do.	Labium

With regard to the first and third segments further comment is necessary. The ocular segment is clearly established on account of its well-defined neuromere, but cœlom sacs and appendages have only so far been detected among insects in the embryo of *Carausius* by Wiesmann : they are also present according to Heymons in the embryo of *Scolopendra.* The intercalary segment bears reduced appendages in the embryos of many insects. In *Campodea* (Uzel) and the grasshopper *Dissosteira* (Snodgrass) rudiments which appear to represent these appendages are discernible in the adult.

Hanström (1928), from a comparative study of the brain in Annelida and Arthropoda, claims that in the latter animals the brain consists of two ganglia only. The protocerebrum and deutocerebrum he regards as being secondarily differentiated from the annelid archicerebrum while the tritocerebrum is claimed to represent the first pair of post-oral ganglia which have fused with it. The balance of evidence, however, is against his theory which implies a head consisting of a prostomium and four segments in the Insecta.

The theory of a 7-segmented insect head is due mainly to Folsom (1900), whose claim that a neuromere exists between those of the mandibles and maxillæ has not been substantiated on embryological grounds. Hansen's view (1930) that maxillulæ occur as true appendages in the Apterygota, and coexist with paragnaths but are not homologous with them implies the existence of four gnathal segments, but this theory similarly lacks embryological support.

Further information on the segmentation of the insect head, together with references to the literature, will be found in papers listed under Embryology, p. 186.

(*e*) Literature on the Head and Mouth-Parts

BÖRNER, 1921.–Die Gliedmassen der Arthropoden. In Lang's *Handbuch der wirbellosen Tiere*. 4. **BUGNION, 1920.**–Les Parties Buccales de la Blatte. *Ann. Sci. Nat. Zool.* **CRAMPTON, 1921.**–The Origin and Homologies of the so-called "Superlinguæ" or "Paraglossæ" (Paragnaths) of Insects and related Arthropods. *Psyche*. 28. —— **1921A.**–The Sclerites of the Head and the Mouth-parts of certain immature and adult Insects. *Ann. Ent. Soc. Am.* 14. —— **1922.**–A Comparison of the First Maxillæ of Apterygotan Insects and Crustacea from the Standpoint of Phylogeny. *Proc. Ent. Soc. Washington* 24. —— **1925.**–The external anatomy of the Head and Abdomen of the Roach, *Periplaneta americana*. *Psyche*, 32. —— **1928.**–The eulabium, mentum, submentum and gular region of insects. *Journ. Ent. and Zool.* 21. **EVANS, 1921.**–On the Structure and Occurrence of Maxillulæ in the Orders of Insects. *Journ. Linn. Soc. Zool.* 34. **FOLSOM, 1900.**–The Development of the Mouth-Parts of *Anurida maritima* Guer. *Bull. Mus. Comp. Zool. Havard*, 36. **GOODRICH, 1897.**–On the Relation of the Arthropod Head to the Annelid Prostomium. *Quart. Journ. Micros. Sci.* 40. **HANDSCHIN, 1929.**–Ein neuer Rüsseltypus bei einem käfer. *Zeits. Morph. u. Ökol. der Tiere.* 14. **HANSEN, 1893.**–A Contribution to the Morphology of the Limbs and Mouth Parts of Crustaceans and Insects. *Ann. Mag. Nat. Hist. ser.* 6, 12. (Trans. from *Zool. Anz.* 16.) —— **1930.** –Studies on Arthropoda. III. Copenhagen. **HANSTRÖM, 1928.**–Vergleichenden Anatomie des Nervensystems de wirbellosen Tiere. Berlin. **JANET, 1899.**–Essai sur le constitution morphologique de la tête de l'insecte. Paris. **KELLOGG, 1902.**–The Development and Homologies of the Mouth-Parts of Insects. *Amer. Nat.* 36. **SNODGRASS, 1928.**–Morphology and Evolution of the Insect Head and its Appendages. *Smiths. Misc. Coll.* 81, No. 3. —— **1932.**–Evolution of the Insect Head and the Organs of Feeding. *Smithsonian Rep.* 1931 : 3160. **WALKER, 1931.**–On the Clypeus and Labium of primitive Insects. *Canad. Ent.* 63. **YUASA, 1920.**–The Anatomy of the Head and Mouth-Parts of Orthoptera and Euplexoptera. *Journl. Morph.* 33.

(*f*) The Cervicum or Neck Region

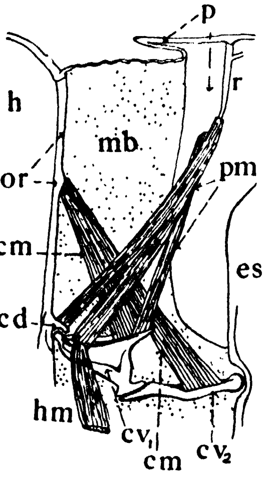

FIG. 15.—NECK AND CERVICAL SCLERITES OF A GRASSHOPPER. (*DISSOSTEIRA.*)

cd, occipital condyle ; *es*, episternum ; cephalic (*cm*), protergal (*pm*) and prosternal (*hm*) muscles of cervical sclerites (cv_1, cv_2) ; *h*, head ; *p*, protergum ; *por*, postoccipital rim ; *r*, ridge of protergum. From Snodgrass.

The cervicum is the flexible intersegmental region between the head and the prothorax (Fig. 1). In its membrane are embedded a variable number of small plates termed *cervical sclerites* (Fig. 18). The latter are present in nearly all orders of insects but are best developed in the more primitive groups (Orthoptera, Dermaptera, Isoptera, Odonata, etc.) : in the higher orders they occur in a more or less reduced condition. In their least modified form the cervical sclerites consist of paired dorsal, lateral, and ventral plates of which the lateral pair is of special importance. The lateral sclerites usually comprise two plates on either side which are closely hinged together so as to form a fulcrum between the head and prothorax. The distal plate articulates with the occipital condyle of the head, while the proximal plate is hinged to the prothoracic episternum (Fig. 15). Levator muscles arising from the postoccipital rim and from the prothoracic tergum are attached to the lateral cervical sclerites of their side. The contraction of these muscles widens the angle between the two plates of a pair and, in this way, causes the protraction of the head.

The morphological nature of the cervicum is highly problematical and the available evidence suggests that something more than an enlarged intersegmental region may be involved. According to Snodgrass (1932) there is some embryological support for the view that the postoccipital rim is a remnant of the labial segment and that a posterior membranous part of this region together with the anterior part of the prothorax enter into the formation of the neck.

Literature

VERHOEFF, 1902.–Uber Dermapteren l. Aufsatz: Versuch eines neuen natürlichen Systems auf vergleichend-morphologischer Grundlage und den Mikrothorax der Insekten. *Zool. Anz.* 25. **CRAMPTON, 1917.**–The Nature of the Veracervix or Neck Region in Insects. *Ann. Ent. Soc. Am.* **10.** **SNODGRASS, 1932.**–Vide p. 24.

THE THORAX

(*a*) Segmentation of the Thorax

THE essential morphology of the thorax was first clearly interpreted by Audouin in 1824 who pointed out that it is composed of three segments, the *pro-*, *meso-*, and *meta-thorax*. This conclusion has received the confirmation of subsequent morphological and embryological research, while the composite-segment theories of Kolbe, Verhoeff and others lack sufficient support, and can only be regarded as untenable. In almost all insects each segment bears a pair of legs and, in the majority of adult insects, both the meso- and metathorax carry a pair of wings. In all cases where the legs are wanting, their absence is due to atrophy. This apodous condition is extremely rare among the imagines but it is the rule among the larvæ of the Diptera, and also those of certain families of Coleoptera. All hymenopterous larvæ, excepting those of the sub-order Symphyta, are similarly devoid of legs. The absence of wings, on the other hand, may be an ancestral character as in the Apterygota, but among the Pterygota it is always an acquired feature due to the atrophy of pre-existing organs. The thorax is exhibited in its simplest form in the Thysanura, in certain of the more generalized Pterygota and in the larvæ of many orders. In these instances the segments differ but little in size and proportions, but usually with the acquirement of wings, a correlated specialization of the thorax results. The meso- and metathorax become more or less intimately welded together and the union is often so close that the limits of those regions can only be ascertained with difficulty. In orders where the wings are of about equal area these two thoracic segments are of equal size (Isoptera, Embioptera, Odonata, etc.). Where the fore wings are markedly larger than the hind pair there is a correspondingly greater development of the mesothorax (Hymenoptera, and also Diptera where the hind wings are absent). In cases where the fore-wings are small there is a correlated reduction of the mesothorax (Coleoptera). The prothorax never bears wings and is also variable in its degree of development. Its dorsal region may be enlarged to form a shield as in the Orthoptera, Coleoptera and Hemiptera-Heteroptera : in most other orders it is reduced to a narrow annular segment.

(*b*) The Sclerites of a Thoracic Segment

When describing the sclerites and regions of the thorax the prefixes *pro*, *meso*, and *meta* are used according to the segment to which the reference applies. Thus the expression protergum refers to the tergum of the prothorax and mesepimeron to the epimeron of the mesothorax. The prefixes *pre* and *post* are also used to designate certain sclerites of any one of the segments and in such cases the prefixes pro, meso, and meta are usually not applied. For example the prescutum may be present on each thoracic segment in front of the scutum.

The **Tergites**.—In many larvæ and pupæ, and also in the adults of certain of the more generalized insects, the tergum of each segment is a simple undivided plate or *notum*. In the wing-bearing segments of most adult Pterygota the tergum is composed of a large anterior plate or notum already mentioned, and a narrower posterior plate or *postnotum* (postscutellum or pseudonotum of some authors) which has arisen in the intersegmental membrane. The notum is typically divided into three sclerites,—the *prescutum*, the *scutum* and the *scutellum* (Fig. 16). At the sides of the pronotum in many Lepidoptera are lobe-like structures known as *patagia*.

The **Pleurites** (Figs. 17–19).—The pleuron consists of an anterior sclerite or *episternum* and a posterior sclerite or *epimeron*, the two being separated by the *pleural suture*. In many insects, however, deviations from this simple condition are evident owing to the subdivision of the pleurites into secondary plates, or their fusion with other regions of their segment. The anterior part of the episternum is frequently marked off as a separate plate, the *pre-episternum*, which is mainly present in the lower orders. In many insects (*Chrysopa, Corydalis, Tipula, Tabanus*) the episternum is divided into an upper and lower sclerite. These two sclerites have been termed by Packard the *supra-episternum* and *infra-episternum* respectively. Not infrequently the lower portion of the episternum is fused up with the sternum, as in Diptera, and the compound plate thus formed is the *sterno-pleurite* (Crampton) or *sternopleura* (Östen Sacken). The epimeron, likewise, is sometimes divided into two sclerites by a transverse suture. A recognized terminology applicable to these sclerites similarly does not exist; for the upper plate the name *supra-epimeron* (or pteropleura) and the name *infra-epimeron* for the lower plate may be adopted. When the pleron as a whole is fused with the sternum the combined sclerite is known as the *pectus*. In many of the higher insects the pleuron is usually connected

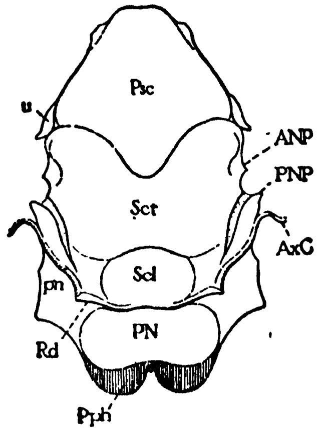

FIG. 16.—MESOTERGUM OF A CRANEFLY, SHOWING DIVISION OF NOTUM INTO THREE SCLERITES (*Psc*, *Sct*, and *Scl*) BEHIND WHICH IS POSTNOTUM (*PN*).

AxC, axillary cord; *ANP*, anterior notal wing process; *PN*, *pn*, postnotum; *PNP*, posterior notal wing process; *Pph*, post-phragma; *Psc*, prescutum; *Rd*, posterior reduplication of notum; *Scl*, scutellum; *Sct*, scutum; *u*, lobe of prescutum before base of wing. After Snodgrass, *Proc. U.S. Nat. Mus.* 39.

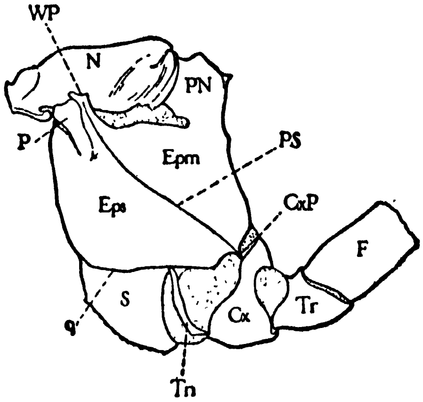

FIG. 17.—METATHORAX OF A STONEFLY, LEFT SIDE.

Cx, coxa; *CxP*, pleural coxal process; *Epm*, epimeron; *Eps*, episternum; *F*, base of femur; *N*, notum; *P*, episternal parapterum; *PN*, post notum; *PS*, pleural suture; *q*, sterno-pleural suture; *S*, sternum; *Tn*, trochantin; *Tr*, trochanter; *WP*, pleural wing process. After Snodgrass, *loc. cit.*

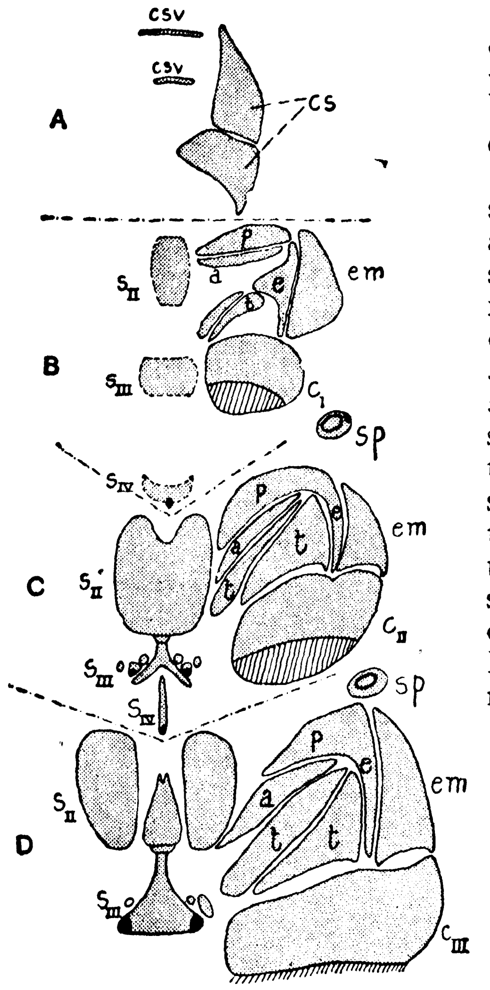

Fig. 18.—Sternal and Pleural Sclerites of Cervicum and Thorax of *Blatta*.

A, Cervicum. B, Prothorax. C, Mesothorax. D. Metathorax. *a*, ante-coxal piece; *c*I–*c*III, coxae; *cs*, lateral cervical sclerites; *csv*, ventral ditto; *e*, episternum; *em*, epimeron; *p*, pre-coxal bridge; *sp*, spiracle; *s*II, eusternum; *s*III, sternellum; *s*IV, poststernellum; *t t*, trochantin.

and fused with the tergum by means of downward prolongations of the prescutum and postnotum.

The **Sternites**.—The nomenclature of the sternites dates from MacLeay, 1830, who believed that each thoracic segment is composed of four segments and, therefore, concluded that the sternum is similarly divided in a fourfold manner. He accordingly introduced the now well-known terms *presternum, sternum, sternellum* and *poststernellum* for the presumed subdivisions. Snodgrass (1909) adopted the term *eusternum* in place of the expression sternum as the latter refers to all the ventral sclerites of a thoracic segment. In the majority of insects, two sternites are typically present,—the eusternum and sternellum: among Hymenoptera and Coleoptera the sternites may be fused together to form a single compound sclerite. The *eusternum* is a large sclerite of variable shape and frequently extends laterally and upwards into the pleural region; at its sides there may be separate plates (*latero-sternites* of Crampton) as in Isoptera and Dermaptera. The laterosternite may become united with the episternum of its side to form the *precoxal bridge.* The *presternum* lies in front of the eusternum and in all probability is derived from it: it occurs in the prothorax of *Ectobia* and *Forficula* and in front of all three

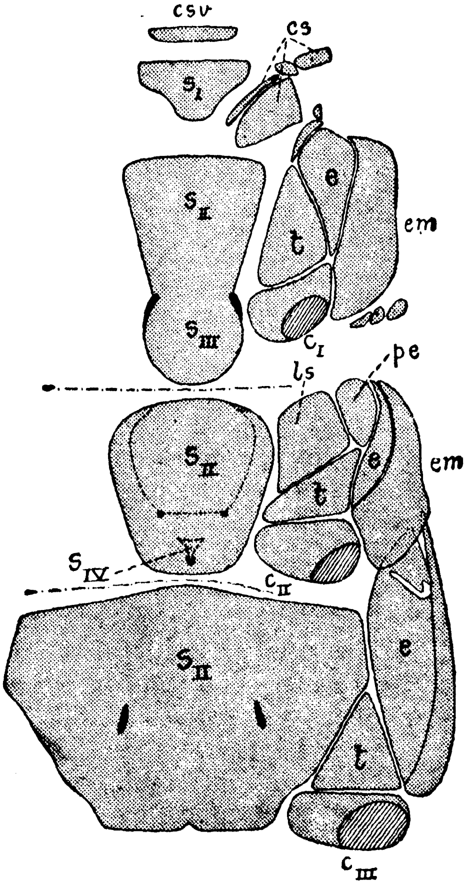

Fig. 19.—Sternal and Pleural Sclerites of *Forficula*.

pe, pre-episternum; *ls*, laterosternite; s_1, presternum. Other lettering as in Fig. 18.

thoracic segments of *Capnia* and *Leuctra* (Crampton). The *sternellum* is the sclerite immediately behind the eusternum and frequently bears the *furca* (vide p. 53). Although usually fused with the eusternum, it is distinct in all three segments of *Capnia*, and in the prothorax of *Periplaneta*. The *poststernellum*, as its name implies, lies behind the sternellum and may bear a median apodeme or *spina*. As this sclerite is often fused, either with the segment in front or behind, it is probably to be regarded as one of the ventral intersegmentalia.

(*c*) The Legs

The legs are primarily organs for running or walking and are well represented in their normal condition in a Cicindelid or Carabid beetle. They exhibit, however, a wide range of adaptive modifications in different families (Fig. 20). Thus in *Gryllotalpa* and the Scarabæidæ the fore-legs are modified

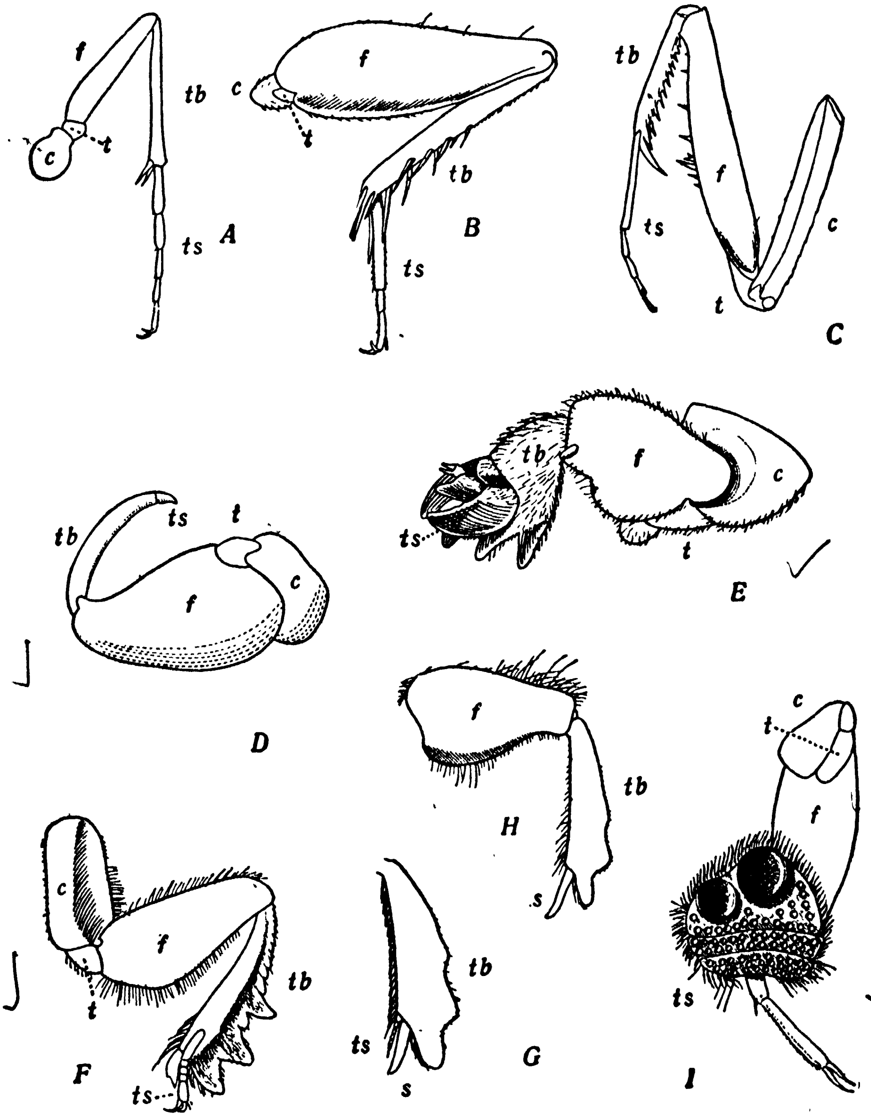

FIG. 20.—ADAPTIVE MODIFICATIONS OF THE LEGS.

A, *Cicindela sexguttata* ; *B*, *Nemobius vittatus*, hind leg ; *C*, *Stagmomantis carolina*, left fore-leg ; *D*, *Pelocoris femoratus*, right fore-leg ; *E*, *Gryllotalpa borealis*, left fore-leg ; *F*, *Canthon lævis*, right fore-leg ; *G*, *Phanæus carnifex*, fore tibia and tarsus of female ; *H*, *P. carnifex*, fore tibia of male ; *I*, *Dytiscus fasciventris*, right fore-leg of male ; *c*, coxa ; *f*, femur ; *s*, spur ; *t*, trochanter ; *tb*, tibia ; *ts*, tarsus. *After* Folsom, 1923.

for burrowing, and in the Mantidæ for seizing and holding the prey. In certain families of butterflies the forelegs are so much reduced that in these insects there are only two pairs of functional limbs. In the saltatorial Orthoptera, and *Phyllotreta* and other genera of Coleoptera, the hind femora are greatly enlarged in order to accommodate the powerful extensor muscles which are used in leaping. Among the Odonata all the legs are adapted for seizing and retaining the prey and are scarcely, if ever, used for locomotory purposes, while in the Bombyliidæ the slender legs are used for alighting rather than walking. In aquatic insects they are often specially adapted as swimming organs. Each leg (Fig. 22) consists of the following parts,—*coxa, trochanter, femur, tibia* and *tarsus* together with certain basal or *articular sclerites.*

The **Basal Articulations of the Legs** (Figs. 17 and 19).—The coxa or proximal joint of the leg articulates with the body by means of the coxal process of the pleuron and with the trochantin when the latter sclerite is present. The *coxal process* is situated at the ventral extremity of the pleural suture. The *trochantin* is the articular sclerite situated at the base of the coxa in the more primitive orders. It frequently unites with neighbouring sclerites, or it may be divided into a pair of plates. Between the single or divided trochantin and the episternum, or between the trochantin and the precoxal bridge, there is frequently an inner sclerite or *antecoxal piece.* The homologies of these small basal sclerites in different insects have been much discussed and it is probable that they are derived from an original subcoxa (see below).

The **Subcoxa** is the true basal segment of the primitive leg, but it is either reduced or much modified in all insects. It is only rarely represented by an undivided sclerite as in *Machilis* (Fig. 225) and a few other Apterygota where pleural sclerites are undeveloped. Among the Pterygota, Hansen (1930) regards the trochantin as its sole remnant, but it is more generally conceded that this sclerite is only a small part of the subcoxa, the major part probably having become incorporated into the thoracic wall to form the pleural sclerites (vide Snodgrass, 1929). This view is supported by the condition found among Apterygota and in certain immature Pterygota. Thus, in the cicada (*Tibicina*) the large subcoxa shows differentiation into rudimentary pleurites with a small basal piece or *trochantin* (Fig. 21).

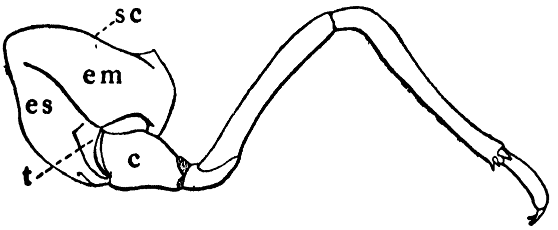

FIG. 21.—HIND LEG AND PLEURON OF MATURE NYMPH OF *TIBICINA SEPTENDECIM.*

c, coxa; *em*, epimeron; *es*, episternum; *sc*, subcoxa; *t*, trochantin. *After* Snodgrass.

The **Coxa** has replaced the subcoxa as the functional base of the leg. It is frequently divisible into two lobes by an inflexion of its wall where it articulates with the pleuron. The posterior lobe thus delimited is the *meron* which is usually the larger part of the coxa. A meron is well developed in *Periplaneta,* the Isoptera, Neuroptera and Lepidoptera.

The **Trochanter** is the second division of the leg: it articulates with the coxa but is usually rigidly fixed to the femur. In the Odonata it is divided into two subsegments and among the parasitic Hymenoptera a second trochanter, derived from the base of the femur, is present.

The **Femur.**—The femur usually forms the largest region of the leg and is especially conspicuous in most insects which have the power of leaping.

The **Tibia.**—The fourth division of the leg is known as the tibia: it is almost always slender and frequently equals or exceeds the femur in length. Near its distal extremity it carries one or more *tibial spurs*. In many Hymenoptera the enlarged apical spur of the anterior tibiæ fits against a pectinated semi-circular pit in the first tarsal joint, and the antennæ are passed between these two organs for cleaning purposes.

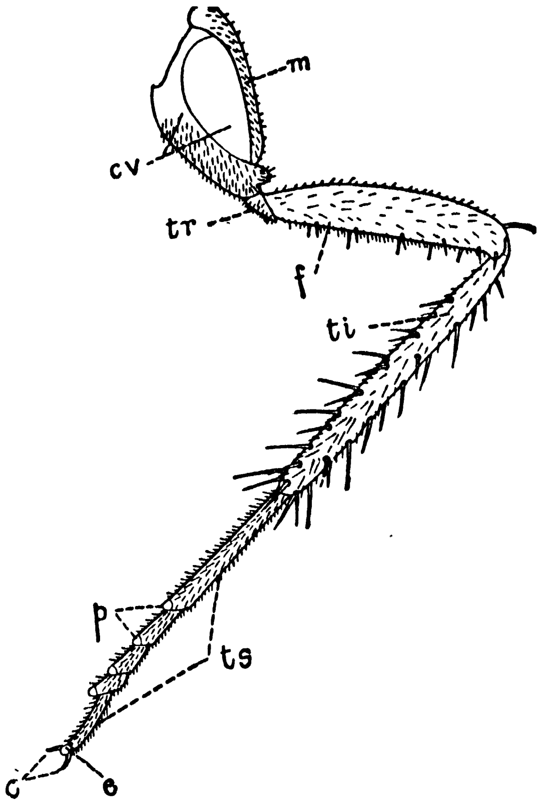

Fig. 22.—A Typical Leg of an Insect (Left) Hind-leg of *Blatta*).

cv, coxa vera; *m*, meron; *tr*, trochanter; *f*, femur; *ti*, tibia; *ts*, tarsus; *c*, claws; *e*, arolium; *p*, plantulæ.

The **Tarsus** consists primitively of a single segment, a feature of which is present in the Protura, entognathous Thysanura and in some larvæ. More usually it is divided into subsegments, typically five in number, but none of these subsegments have acquired muscles and movement of the tarsus as a whole is effected by flexor muscles arising from the tibia or femur. At its apex the tarsus bears a group of structures forming the *pretarsus* (de Meijere, 1901) which represents the terminal segment of the leg. In its simplest condition, seen in Collembola, Protura and many larvæ, the pretarsus is prolonged into a single claw. In most insects the claws are paired and between them, on the ventral side, the pretarsus is supported by a median *flexor plate* to which the tendon of the flexor muscle of the claws is attached. In front of and above this plate the pretarsus expands into a median lobe or *arolium* (Fig. 23). Among Diptera there are two lobes or *puvilli* lying below the claws, often with an arolium between them or, in place of an arolium, the flexor plate itself is prolonged into a median bristle or *empodium* (Fig. 24). On the underside of the tarsal joints there are frequently pulvillus-like organs or *plantulæ* (Fig. 22). The arolium and pulvilli are pad-like organs enabling their possessors to climb smooth or steep surfaces: the plantulæ also have a similar function. Such organs are outgrowths of the parts from which they arise and their cavities contain blood. Various explanations have been offered as to how they function

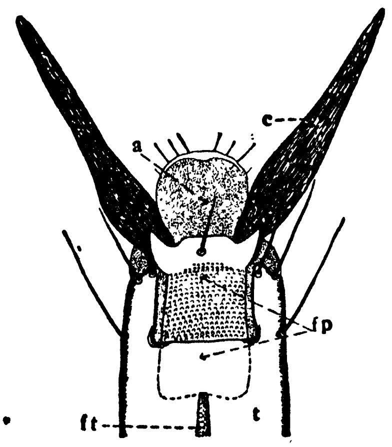

Fig. 23.—Pretarsus of an Orthopteron, ventral view.

a, arolium; *c*, claw; *fp*, flexor plate; *ft*, tendon of flexor muscle; *t*, tarsus.

(Dewitz 1884, Dahl 1884) and among recent investigators are Arnhardt (1923) and Gillett and Wigglesworth (1932). In the hivebee Arnhardt states that the arolia function by adhesion to the surface upon which the insect climbs, the ventral face of the arolium being moistened by a sticky secretion exuded by tenant hairs immediately behind. In *Rhodnius* (Reduviidæ) Gillett and Wigglesworth found that the tibial plantulæ are closely covered with tenant hairs of peculiar form and that ability to climb probably depends upon the adhesion of such hairs to a given surface. This same method of functioning probably prevails in many other insects.

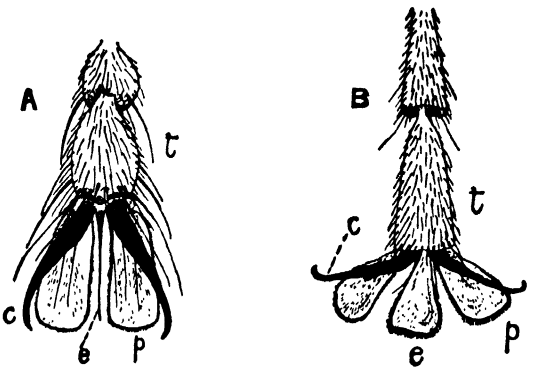

FIG. 24.—FEET OF THE MALES OF A, *ASILUS CRABRONIFORMIS*; B, *LEPTIS NOTATA*.

c, claw; *e*, in A, empodium: in B, arolium; *p*, pulvillus; *t*, last tarsal joint. *After* Verrall.

Locomotion (Terrestrial).—During walking an insect usually moves its legs in two series in such a manner that the fore- and hind-legs of one side, and the middle leg of the opposite side, progress forward almost synchronously. By this means the body is supported as it were for the moment on a tripod formed by the remaining three legs. The anterior leg functions as an organ of traction: having extended and fixed its claws, it pulls the body forwards by means of the contraction of the flexor muscle of the tibia. The function of the hind leg is mainly that of pushing the body forwards, while the middle leg serves to support and steady the body and determines its movement in the vertical plane (Demoor, 1890). For detailed information on the subject of terrestrial locomotion, and the mechanics of the process, reference should be made to the text-books of Packard and Schröder.

(*d*) The Wings

The presence of wings is one of the most characteristic features of insects, and the dominance of the latter as a class is to be attributed to the possession of these organs. Owing to their wide range of differentiation, wings provide one of the most useful characters for purposes of classification. In virtue of its more or less triangular form the wing of an insect presents three margins (Fig. 25): the *anterior margin* or *costa* (*a–b*); the *outer* or *apical margin* (*b–c*) and the *inner* or *anal margin* (*c–d*). Three well-defined angles are also recognizable, viz., the *humeral angle* (*a*) at the base of the costa; the *apex* (*b*) or angle between the costal and outer margins and the *anal angle* (*c*) between the outer and inner margins. Although, in the greater number of insects, the wings appear to be naked, in many cases microscopical examination reveals the presence of fine hairs. On the other hand, in certain groups the wings are obviously clothed. In the Trichoptera and the dipterous family Psychodidæ, for example, they are closely

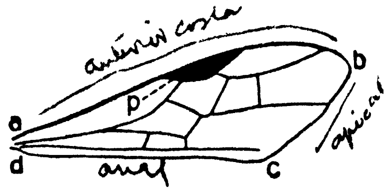

FIG. 25.—WING OF A HYMENOPTERON (explanation given in the text).

p, pterostigma.

covered with hairs, while in the Lepidoptera the wings are invested with overlapping scales.

Tillyard (1918A) has made a study of the hairs occurring on the wings of the most primitive groups of the Holometabola. *Microtrichia* are found indiscriminately on the wing-membrane and veins alike. *Macrotrichia* or true setæ, which have annular bases of insertion, are found on the main veins and their branches, on the archedictyon (p. 41), less frequently on the wing membrane and very rarely on the cross-veins. On the disappearance of the archedictyon, or of an individual vein, the macrotrichia may persist on the wing membrane in their original positions ; their presence thereon is regarded by Tillyard as evidence of descent from more densely veined ancestors. By plotting the positions of the macrotrichia present on the wing membrane in such primitive forms as *Archichauloides*, *Rhyacophila* and *Rhyphus*, and joining them up into a polygonal meshwork, the lost archedictyon can often, to some extent, be reconstructed (Fig. 26).

A conspicuous opaque spot is found near the costal margin of the wing in many insects, and is termed the *stigma* or *pterostigma* (Fig. 25). It is present, for example, in the fore-wings of the Psocoptera, and most Hymenoptera, and in both pairs of wings of the Odonata.

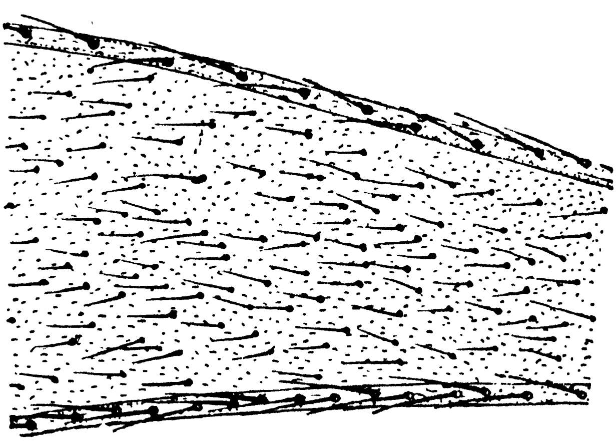

FIG. 26.—PORTION OF A WING OF *RHYPHUS BREVIS* SHOWING MACROTRICHIA AND MICROTRICHIA. *After* Tillyard, *Proc. Linn. Soc. N.S.W.* 43.

The **Basal Attachment and Articular Sclerites of the Wings.**—Each wing is hinged to two processes of the notum of its segment, the *anterior notal process* and the *posterior notal process* (Fig. 27, A). The wing also articulates below with the *pleural wing process*. The posterior margin of the membrane at the base of the wing is frequently strengthened to form a cord-like structure known as the *axillary cord*. The latter arises, on either side, from the posterior lateral angle of the notum (Fig. 27, A).

Situated around the base of each wing is a variable number of *articular sclerites* which consist of the tegulæ and the axillaries (Fig. 27). The *tegulæ* (paraptera of some authors) are a pair of small scale-like sclerites carried at the extreme base of the costa of each fore-wing : they are rarely present in connection with the hind-wings. Tegulæ are best developed in the Lepidoptera, Hymenoptera, and Diptera, being especially large in the first mentioned order. The *axillaries* (pteralia) participate in the formation of the complex joint by which the wing is articulated to the thorax. According to Snodgrass they occur in all winged insects but are much reduced in the Ephemeroptera and Odonata : in the two latter orders the wing base is directly continuous with the notum. As a rule, three of these sclerites are present, but a fourth occurs in the Orthoptera and Hymenoptera. The *first axillary* articulates with the anterior notal process and is associated with the base of the sub-costal vein. The *second axillary* articulates partly with the preceding sclerite and, as a rule, partly with the base of the radius (vide p. 39). The *third axillary* usually articulates with the posterior notal process. When a *fourth axillary* occurs it has a double articulation, i.e., with the posterior notal process proximally and with the third axillary distally. For a more detailed treatment of these sclerites vide Snodgrass (1929).

In addition to the foregoing, there are present in many insects small epipleural sclerites which are located below the insertions of the wings (Fig. 27). Although they are regarded as parts of the pleura they may be conveniently referred to here on account of their close association with the wing attachments. These sclerites are separated into two series by the pleural wing process. The anterior or *basalar sclerites* are never more than two in number, and lie just above the episternum, while the posterior or *subalar sclerite* is almost always single and lies behind the pleural wing process and above the epimeron.

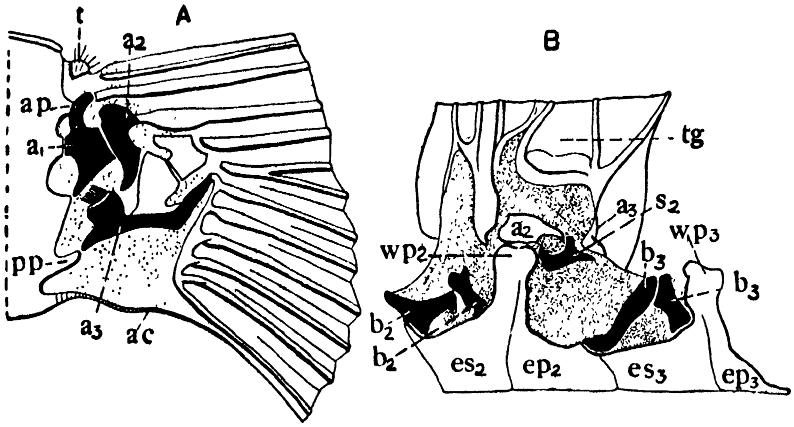

FIG. 27.—BASAL ARTICULATIONS OF THE WINGS. A. WING BASE AND TERGAL ARTICULATION. B. UPPER PART OF PLEURON OF A GRASSHOPPER WITH BASE OF LEFT TEGMEN (*tg*) UPRAISED.

a_1–a_3, axillary sclerites ; *ac*, axillary cord ; *ap*, anterior notal wing process ; b_2, basalar sclerites of mesothorax ; b_3, basalar sclerites of metathorax ; ep_2, epimeron of mesothorax ; ep_3, epimeron of metathorax ; es_2, episternum of mesothorax ; es_3, episternum of metathorax ; *pp*, posterior notal wing process ; S_2, subalar sclerite of mesothorax ; *t*, tegula ; wp_2, pleural wing process of mesothorax ; wp_3, pleural wing process of metathorax. Adapted from Snodgrass.

Modifications of Wings.—Although wings are usually present in adult insects a by no means inconsiderable number of species are apterous. This condition is a constant feature of the Apterygota, where it is a primitive character, but in the Pterygota the loss of wings has been secondarily acquired. The parasitic orders Anoplura and Aphaniptera are exclusively apterous, and the same applies to the sterile castes of the Isoptera and Formicidæ, and to the females of the Coccidæ. Among other Pterygota, apterous forms are of casual occurrence, and often confined to a single sex or species. Thus, in the moth *Hybernia defoliaria,* and most Embiidæ, the females alone are apterous, while in the Chalcid genus *Blastophaga* it is the male which has lost the wings. Transitional forms between the apterous and the fully winged condition are found. In the moth *Diurnea fagella,* for example, the wings of the female are lanceolate appendages, but little more than half the length of those of the male, and useless for flight. In the winter moths (*Cheimatobia*), and in the fly *Clunio marinus,* they are reduced in the female to the condition of small flap-like vestiges.

Throughout the Diptera, and in the males of the Coccidæ, the hind wings are wanting, and are represented only by a pair of slender processes which, in the Diptera, are termed *halteres.* Among the Coleoptera, the fore-wings are much hardened to form horny sheaths or *elytra,* which protect the hind-wings when the latter are in repose. In the genus *Attractocerus,* and the males of the Stylopidæ, the elytra are reduced to the condition of small scale-like appendages. On the other hand, in certain Carabidæ and Curculionidæ, the hind-wings are atrophied and the function of flight is lost. In the Heteroptera the fore-wings are thickened at their bases like elytra and, for this reason, are frequently termed *hemelytra*. Among the Orthoptera, the fore-wings are hardened and of a leathery consistency, being known by many writers as *tegmina*.

The **Wing-Coupling Apparatus.**—There seems little doubt that, in the primitive Pterygota, the fore and hind pair of wings moved independently of each other, and that coincidence of motion was a later acquisition, consequent upon the development of a wing-coupling apparatus. The studies of Tillyard (1918) indicate that, in those orders in which the wings were more or less hairy, the marginal macrotrichia probably became specialized and localized to form a locking mechanism. The most archaic form of the latter consisted of a projecting bristle-bearing area or lobe on the hind margin of the fore-wing and a very similar structure on the costal margin of the hind-wing. Thus, in the fore-wing the backwardly projecting area of contact with the hind-wing is the *jugal lobe*, bearing a series of *jugal bristles*: similarly, the area of contact of the hind-wing with the fore-wing is the *humeral lobe*, and the bristles projecting therefrom constitute the *frenulum* (Fig. 28). The wings of a side are interlocked by the frenulum projecting *beneath* the jugal lobe of the fore-wing, and the jugal bristles lying above the costa of the hind-wing. The nearest approach to this archaic condition is exhibited among certain of the Mecoptera. Thus, in *Tæniochorista* the jugal lobe and its bristles are retained unmodified and there is a small definite humeral lobe, but the frenulum is reduced to the condition of two very powerful bristles (Fig. 28, B). In most of the Hymenoptera the costal margin of the hind-wing bears a series of hooks or *hamuli*, whose function is to grasp a ridge-like thickening along the inner margin of the fore-wing. In the majority of the Lepidoptera the wings are held together by means of the *frenulum* which is maintained in place by a kind of catch or *retinaculum* on the fore-wing (Fig. 28, D). In moths of the family Hepialidæ the jugal lobe or jugum of the fore-wing projects beneath the hind-wing and, owing to the greater part of the inner margin of the fore-wing overlapping the hind-wing the wings in this manner become interlocked (Fig. 28, C).

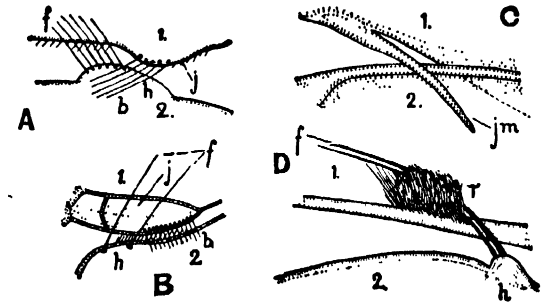

FIG. 28.—TYPES OF WING-COUPLING APPARATUS.

A, hypothetical generalized type. B, Mecoptera (*Tæniochorista*); C, Hepialidæ (*Charagia*); D, Noctuidæ (*Plusia*). 1, fore-wing; 2, hind-wing; *j*, jugal lobe; *jm*, jugum; *b*, jugal bristles; *h*, humeral lobe; *f*, frenulum; *r*, retinaculum. *After* Tillyard, *Proc. Linn. Soc. N.S.W.* 43.

The **Structure and Development of Wings.**—Wings are thin plate-like expansions of the integument which are strengthened by a framework of hollow chitinous tubes known as *veins* or *nervures*. A wing is composed of upper and lower layers which may readily be separated in an insect which has just emerged from the pupa. Viewed in transverse section (Fig. 29), the veins are seen to be much more strongly chitinized than the wing membrane and each, as a rule, encloses a small central trachea. A fine nerve fibre accompanies the larger veins of many insects (Mosley, 1871) and a degenerate trachea known as " Semper's rib " is present in Lepidoptera alongside the ordinary trachea within the vein cavity. When an insect emerges from the pupa or nymph, as the case may be, the veins contain blood which has been observed to circulate through them, and even in the fully formed wings the circulation is often still maintained.

At an early stage in formation, wings are seen to be sac-like outgrowths of the body-wall, which they resemble in histological structure. Whether they are tergal or pleural (or both) in nature is a disputed question and the opinions of various observers are conflicting. On the whole the balance of opinion supports the conclusion that they are tergal structures. In the more primitive orders, with incomplete metamorphosis, they arise externally, but among insects with complete metamorphosis they remain within the body until they attain an advanced stage of development.

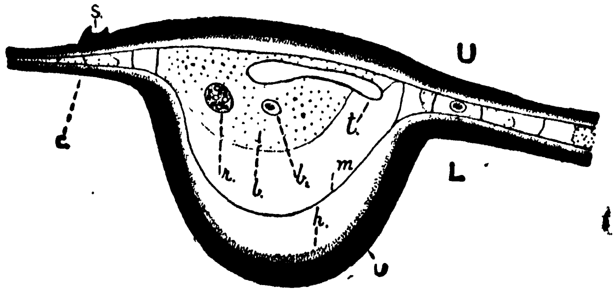

FIG. 29.—TRANSVERSE SECTION OF A VEIN AND ADJACENT PORTION OF THE WING-MEMBRANE OF A MOTH, *NOTODONTA CAMELINA*.

U, upper; L, lower surface; *v*, vein; *h*, remains of hypodermis; *t*, trachea; *c*, cuticle; b_1, blood corpuscle and *b* plasma; *m*, basement membrane; *r*, " Semper's rib "; *s*, scale socket.

In insects with incomplete metamorphosis the wing rudiments first appear externally in post-embryonic life along a line where the suture between the tergum and pleuron later develops (Comstock, 1918). In most nymphs they are so directly continuous with the tergum that they have the appearance of being postero-lateral outgrowths of that region. The external changes during growth are comparatively slight and mainly consist of an increase in size after each moult. When the adult stage is assumed the wings become fully expanded, and the various structural changes are completed. In transverse section (Fig. 30) the developing wing is seen to be invested externally by the cuticle and, lying just beneath the latter, is the hypodermis which is composed for the most part of greatly elongated cells; internally the hypodermis rests upon a basement membrane. During early development tracheal branches enter the wing-buds and extend as the latter enlarge, supplying the growing wings with air. In many places, the basement membrane of the upper and lower layers subsequently meet and fuse, but along the courses of the tracheæ it remains separate, thus demarcating the cavities of the future veins. In a surface view of a developing

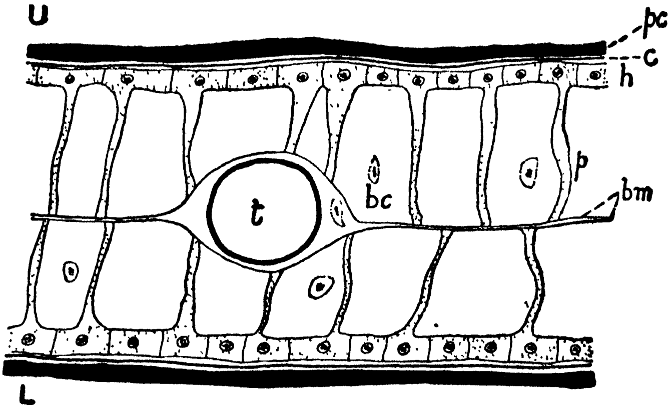

FIG. 30.—TRANSVERSE SECTION OF A PORTION OF THE WING OF A PUPAL INSECT.

U, upper surface; L, lower surface; *pc*, pupal cuticle; *c*, cuticle of developing wing; *h*, hypodermis of wing; *p*, process of hypodermal cell; *bm*, basement membrane; *t*, trachea in cavity of developing vein; *bc*, blood corpuscle.

wing, the vein cavities are seen as paler coloured lines containing blood and tracheæ; in the cavities of the transverse veins tracheæ are wanting. It is important to note that the principal longitudinal veins, as a rule, are

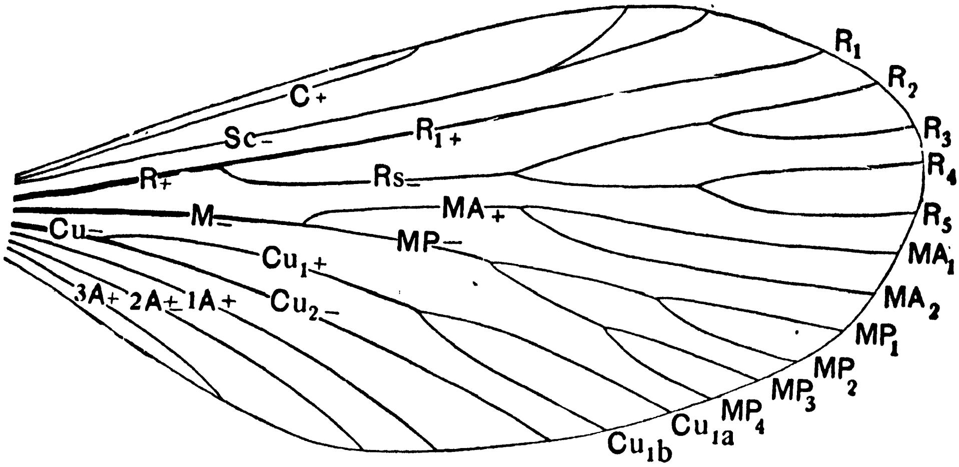

Fig. 31.—Hypothetical Primitive Type of Venation (for reference lettering vide pp. 39 and 40 (convex veins +, concave veins —).

formed about the tracheæ and, as the latter are very constant in number and position, they provide valuable data for determining the homologies of the future wing veins. During the final stages of development the hypodermis secretes the thickened circular walls of the veins and also the wing membrane, but very little trace of its cells persists in the fully expanded wings.

Comstock and Needham (1898–99) have made a comparative study of the wings of nymphs and pupæ which renders it possible to construct the hypothetical tracheation of a wing of a primitive nymph from which the fundamental type of wing venation of each order of insects is presumed to have been derived. Two distinct groups of tracheæ enter the wing—the costo-radial group and the cubito-anal group. This condition is preserved in an almost unmodified form among the Blattidæ, Plecoptera and Homoptera. More usually, however, the two groups are united by a transverse trachea (Fig. 32).

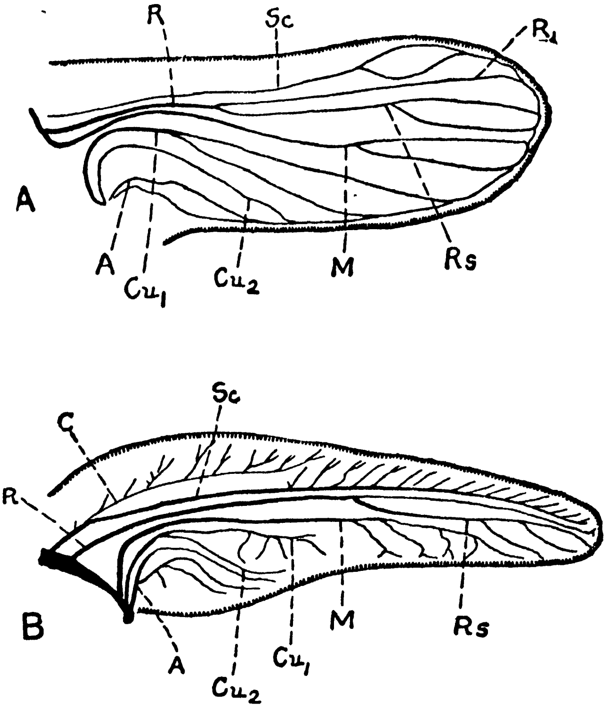

Fig. 32.—Tracheation of Developing Fore-Wings of Nymphs of A. *Nemoura* (Plecoptera) and B. *Conocephalus* (Acridiidæ). Adapted from Comstock. (For explanation of lettering, see p. 39.)

In insects with complete metamorphosis, the development of the wings has been followed much more closely than in the case of the lower orders. It presents many remarkable phenomena which have attracted the attention of numerous investigators, among whom Weismann, Gonin, Kunckel d'Herculais, Pancritius, Mayer and Mercer may be specially mentioned (vide also p. 201). The wings arise from imaginal buds or thickenings of the hypodermis, usually in the neighbourhood of one of the larger tracheæ, and are evident in the very young larva or even the embryo (Fig. 33). These buds become enlarged and invaginated to form pocket-like sacs, or *peripodial cavities* (Fig. 33, *c*), from the bottom of which the thickened portion of the bud ultimately becomes evaginated. At the same time, the walls of the pocket become extremely thin but retain their connection with the hypodermis. At a later stage, the evaginated portion elongates and comes to hang downwards; it is this evaginated portion which, at a later stage, forms the wing. Subsequently, the wing rudiment, as we may term it, becomes pushed out of its pocket and, during the last larval stadium, it comes to lie just beneath the cuticle. On the assumption of the pupal stage, the wing rudiments become evident externally along the sides of the body. When the imago emerges, the wings appear as small wrinkled sacs which gradually become distended by blood pressure, and attain their full development usually several hours afterwards. During their later stages of development the wing buds become supplied with tracheoles. In *Pieris*, for example, during the 4th larval stadium a series of tracheoles arise as proliferations of the epithelium of the large tracheæ associated with the wing bud. These tracheoles may be termed the larval or provisional tracheoles, and they extend in bundles into the developing vein cavities. A little later, the true wing tracheæ develop as tubular outgrowths of the large tracheæ, and extend into the vein cavities along with the larval tracheoles, which they supplant. During the early pupal stage the latter degenerate and disappear. Although the

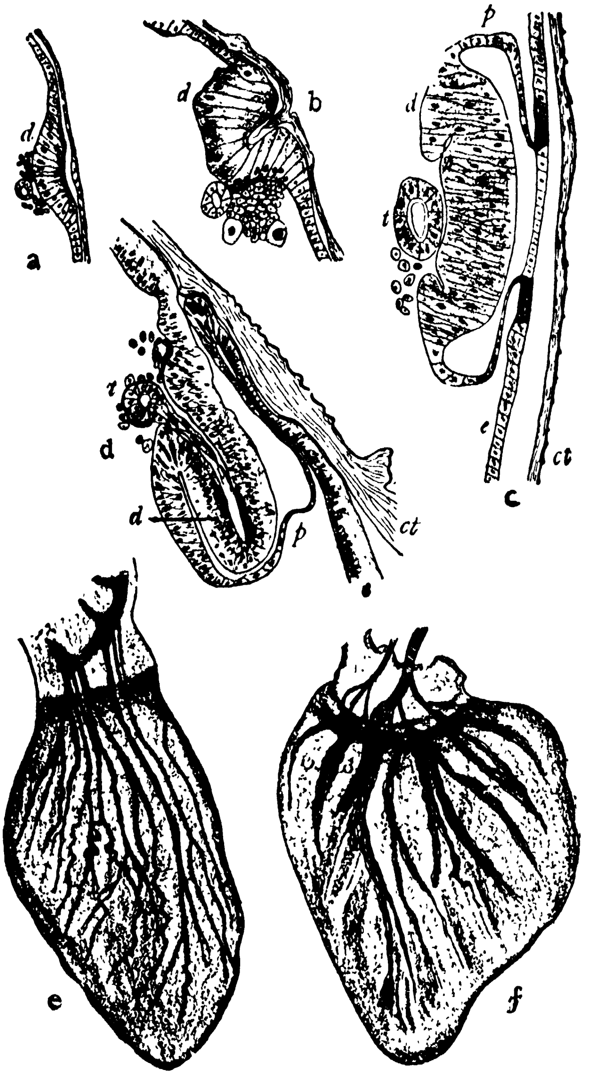

FIG. 33.—SUCCESSIVE STAGES IN THE DEVELOPMENT OF A WING-BUD OF *PIERIS*.

a–d, sections of wing-bud; *e*, *f*, surface views of fore- and hind-wings to show tracheation; *ct*, cuticle; *d*, wing-bud; *e*, hypodermis; *p*, peripodia membrane; *t*, tracheæ. From Comstock, *after* Mercer. (Reproduced from Carpenter "Insect Transformation.")

study of the tracheation of the pupal wings has yielded important data for ascertaining the homologies of the wing veins of the adults, there is a wide divergence in the extent to which the pupal wing-tracheæ correspond with the veins of the imagines. Thus, among the Hymenoptera, specialization may take place to such a degree that the completed wing veins diverge very greatly from the primitive courses of the tracheæ. In these instances, comparison with more generalized types aids in settling the identity of the principal veins.

Venation.—The complete system of veins of a wing is termed its *venation* or *neuration.* The venation presents characters of great systematic importance, but unfortunately the various systems of nomenclature in use are confusing both to the student and the specialist. The establishment of the different systems was made by entomologists whose work was uninfluenced by the modern conceptions of evolution. The result has been that the terminology of an individual author was usually only applicable within the limits of the particular order of insects which he studied. This lack of uniformity has made it incumbent upon the student to learn the particular nomenclature adopted by the authority whose works he may be studying. It is true, efforts have been made to introduce a common terminology for the venation, which shall be uniform throughout the different orders, but, until the work of Comstock and Needham (1898), little success had been achieved. By means of an extensive study of the tracheæ which precede, and in a general sense determine the positions of the veins, these writers have constructed a hypothetical type of venation from which all other types have presumably been derived. Furthermore, among the lower generalized orders the wings are longitudinally plicated after the manner of a partially opened fan. Those veins which follow the ridges are termed *convex veins* and those which follow the furrows *concave veins.* These features are well exhibited not only in the early fossil groups but also in the may-flies, dragon-flies and Orthoptera : in the higher orders they tend to become obscured owing to the flattening of the wing membrane. The fact that the convex or concave condition is constant for individual veins aids in determining their homologies, especially where recourse to tracheation is not possible.

While the researches of Comstock and Needham form the basis for the interpretation of venation their original conceptions have become modified by the more recent work of Lameere, Martynov and Tillyard. The following longitudinal veins (named after the pre-existing tracheæ) may be distinguished, and reference to Fig. 31 shows their relationships and main branches, together with the abbreviations in general use. The *costa* (C) is unbranched and convex while the *subcosta* (Sc) is rarely branched and concave. The *radius* (R) is typically 5-branched : its main stem is convex and divides into two, of which the first branch (R_1) passes directly to the wing margin : the second branch or *radial sector* (Rs) is concave and divides into four veins (R_2 to R_5). The *media* (M) divides into an anterior media (MA), which is convex and 2-branched (MA_1, MA_2), and a concave *posterior media* (MP), which is 4-branched (MP_1 to MP_4). The *cubitus* (Cu) divides into two main branches, the first cubitus (Cu_1) being convex and the second cubitus (Cu_2) concave : the first cubitus subdivides into anterior (Cu_{1a}) and posterior (Cu_{1b}) veins. There follow three *anal veins* ($1A$ to $3A$) which are usually convex, or $2A$ may be concave.

In most insects there are two strongly convex veins, viz. :—R_1 and Cu_1, which are easily noted and therefore facilitate the identification of the other veins. A complete media is found in most Palæozoic fossil insects and in the Ephemeroptera among recent forms. For the most part *MA* atrophies and consequently the media in recent insects is *MP*, although it is usually designated by the symbol *M*. The Odonata, however, are an exception in that they retain *MA* and not *MP*, while further research is needed into the constitution of the media in the Orthoptera and Plecoptera. The anal veins are extremely variable and in wings with a reduced anal area one or more are atrophied. On the other hand, in insects with a well-developed anal lobe the anal veins may be freely branched, but the branching does not appear to be derived from any uniform primitive type.

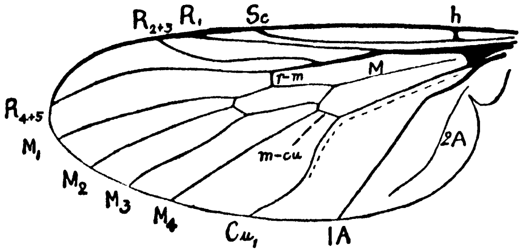

FIG. 34.—WING OF *RHYPHUS PUNCTATUS*. (For explanation of lettering, vide pp. 39 and 41.)

Deviation from the primitive venational type has occurred in two ways, i.e., by reduction and by addition. In many insects the number of veins is less than in the hypothetical type, and the reduction has been brought about by the degeneration or complete atrophy of a vein, or of one or more of its branches, or by the coalescence of adjacent veins. Atrophy explains the presence of only a single well-developed anal vein in *Rhyphus* (Fig. 34) and other Diptera, while the occurrence in this genus of a single vein R_{2+3}, in the place of the two originally separate veins R_2 and R_3 is due to coalescence. Similarly R_4 and R_5 have coalesced, and the single vein thus formed may be conveniently referred to under the abbreviation R_{4+5}. Coalescence takes place in two ways : the point at which two veins diverge may become gradually pushed outwards nearer and nearer the margin of the wing until the latter is reached, and only a single vein remains evident. In the second method, the apices of the two veins may approximate, and ultimately fuse at a point on the wing margin : coalescence of this type takes place inwardly towards the base of the wing. The first type is well exhibited in the case of the radial veins of *Rhyphus*, while the second method is exhibited in the apical fusion of 1A and Cu_1, in *Tabanus* (Fig. 35). The homology of a particular vein is often difficult to determine, and resort has to be made to comparison with allied forms, which exhibit transitional stages in reduction, or to a study of the pupal venation.

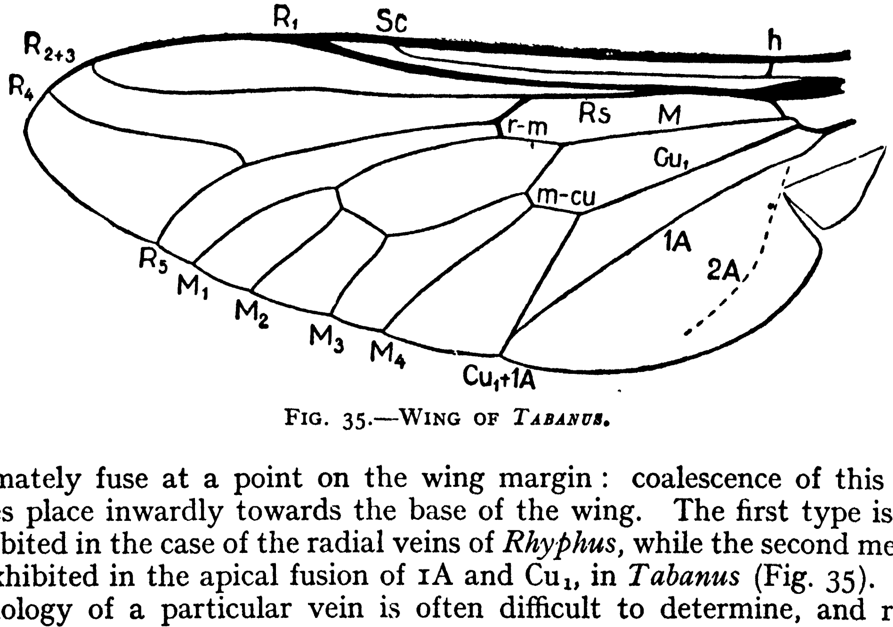

FIG. 35.—WING OF *TABANUS*.

In cases where an increase in the number of veins occurs, the multiplication of the latter is due either to an increase in the number of branches of a principal vein, or to the development of secondary longitudinal veins, between pre-existing veins. In no instance is there any increase in the number of principal veins present. For a more detailed acquaintance with the various modifications of the wing veins the textbook of Comstock (1918) should be consulted.

In the wings of certain of the most generalized insects, such as the fossil Palæodictyoptera, an irregular network of veins is found between the principal longitudinal veins, but no definite cross veins are present (Fig. 36). To this primitive meshwork Tillyard (1918) has given the name *archedictyon.* It appears to have undergone suppression in the Holometabola, though it is very probably homologous with the still-existing dense reticulation present in certain orders of Exopterygota such as the Odonata. Needham (1903) from his studies of the wings of the latter order has discussed the transformation of such an irregular network into regular transverse veins, and reference to Fig. 36 is sufficient to explain his views as to the origin of the latter. Transitional stages in the evolution of definite cross-veins may also be observed in wings of the more specialized Palæodictyoptera and among living Orthoptera, where both irregular and definite cross-veins occur in the same wing. According to Tillyard, however, true cross-veins are later developments; and they are never preceded by tracheæ and are almost always devoid of macrotrichia. Veinlets, on the other hand, are primitive and constitute the finer twigs of a principal vein: they are preceded by tracheæ and carry macrotrichia (Fig. 37). Whether the archedictyon arose in connection with precedent tracheæ in the wing-rudiment, or independently, is unknown. It is probable, therefore, that homologous cross-veins do not exist in many orders: their positions, however, in some cases are so constant that analogies, if not homologies, can be traced and similar names are applicable. The following cross-veins are the most important and their symbols are given in brackets.

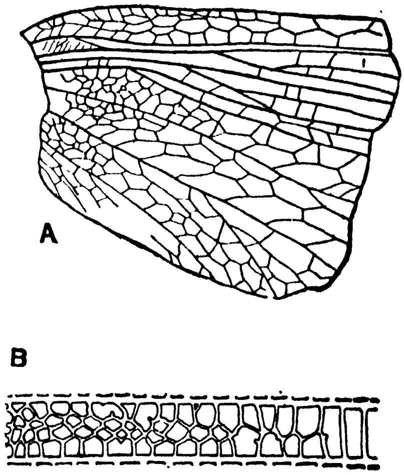

Fig. 36.—A. Portion of a Wing of a Carboniferous Insect (*Hypermegethes*) showing Archedictyon. *After* Handlirsch. B. Diagram illustrating the Evolution of Regular Cross-veins. *After* Needham.

The *humeral cross-vein* (*h*) extending from the sub-costa to the costa, near the humeral angle of the wing.

The *radial cross-vein* (*r*) extending from R_1 to the radial sector (R_s).

The *sectorial cross-vein* (*s*) extending from the stem R_{2+3} to R_{4+5} or from R_3 to R_4.

The *radio-medial cross-vein* (*r–m*) extending from the radius to the media, usually near the middle of the wing.

The *medial cross-vein* (*m*) extending between M_2 and M_3.

The *medio-cubital cross-vein* (*m–cu*) extending from the media to the cubitus.

The veins divide the wings into spaces or *cells.* In the Comstock-Needham system the terminology of the cells is derived from the veins which form their anterior margins. The cells fall into two groups, i.e., basal cells and distal cells. The former are bounded by the principal veins, and the latter by the branches of the forked veins. Thus the cell situated behind the main stem of the radius, near the base of the wing, is cell *R*, while the cell behind the first branch of the radius is designated as cell R_1. When two veins coalesce the cell that was between them becomes obliterated. Thus when veins R_2 and R_3 fuse as in *Rhyphus* (Fig. 34), the cell situated behind the vein R_{2+3} is referred to as cell R_3, and not cell R_{2+3}, cell R_2 having disappeared. Not infrequently two or more adjacent cells may become confluent owing to the atrophy of the vein or veins separating them. The compound cell is then designated by a combination of the abbreviations applied to the originally separate cells. Thus, a cell resulting from the fusion of cells *R* and *M* is referred to as cell $R + M$. The advantage of this relatively simple system of nomenclature is evident in the case of the so-called discal cell for example. The latter expression has been used in at least four separate orders of insects with reference to a different cell in each instance.

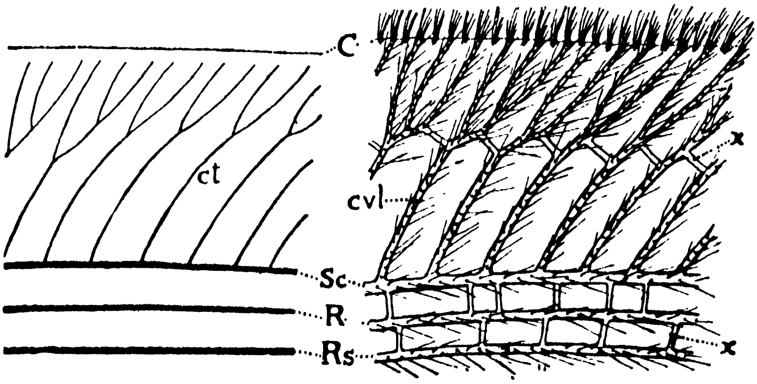

FIG. 37.—PORTION OF COSTAL AREA OF FORE-WING OF *PSYCHOPSIS ELEGANS* WITH THE CORRESPONDING TRACHEATION (TO THE LEFT) OF THE PUPAL WING.

C, costa; *ct*, tracheæ preceding the costal veinlets; *cvl*, costal veinlets; *x*, cross-veins; *R*, radius; *Rs*, radial sector; *Sc*, subcosta. *After* Tillyard, *Proc. Linn. Soc. N.S.W.* 43.

Flight of Insects.—The flight of insects is unlike that found elsewhere in the animal kingdom, not only with regard to the mechanism of flying, but also with reference to the nature of the wing stroke. The researches of Marey (1869) have contributed much towards an exact knowledge of this difficult subject and, among other methods, chronophotography was largely used by this observer. Marey was able to obtain 110 successive photographs per second of a bee in flight but as the wings were vibrating 190 times per second, the images obtained represented isolated though consecutive phases of wing movement. This observer was successful in obtaining clear but isolated images of vibrating wings after an exposure of only $\frac{1}{25,000}$ of a second. According to Marey air-pressure is the main factor which determines the nature of the wing stroke. He concludes that the wing muscles only maintain the to and fro movements of the wings, while the flexibility of the wing membrane, when the latter meets the resistance offered by the air, causes the surface of the wing to be inclined at the most favourable angle. The result is that the path or trajectory made by the apex of the wing takes the form of a continuous series of the figure 8. This was determined by Marey, with the aid of a spangle of gold leaf, fixed to the extremity of a wasp's wing. The insect was then held in the sun with a pair of forceps, in front of a dark background and, under these conditions, a glistening 8-shaped trajectory was observed. The width of the loops of the 8 varies in different insects, and is also dependent upon the speed of motion, and the varying action of the wing muscles. Another factor to be taken into account is the nature of the basal articulations of the wings. It is a matter of controversy whether the articulatory mechanism alone causes the wing to pass through the air, along the course indicated by Marey, or whether the basal articulation is sufficiently flexible to admit of air pressure alone forcing the wing out of what would otherwise have been a simple to and fro motion. Lendenfeld (1881) maintains that the course of the wing is entirely determined by the nature of its basal articulation and the action of the wing muscles. It is not unlikely that among the Odonata, in which the flight mechanism attains a high degree of complexity, these two factors are important contributory causes.

For the purpose of determining the frequency of their movements, wings may be regarded in the same way as vibrating wires. A record thereof may be obtained graphically by means of a revolving cylinder covered with smoked paper, the least contact of the tip of the wing removing the black, and exposing the white paper beneath. If the record thus obtained be compared with one made on the same paper by means of a tuning fork, of an ascertained period of vibration, the frequency of wing movement can be determined with great accuracy. By this method, it was calculated that a house-fly makes 330 strokes per second, a bee 190, a moth (*Macroglossa*) 72, a dragon-fly 28 and a butterfly (*Pieris*) 9 strokes per second. For the flight muscles see p. 58.

Origin of Wings.—Two principal theories have been advanced to account for the origin of wings in insects. (1) The *tracheal gill theory* of Geganbaur which has been upheld by Lubbock, Graber, Lang, Verson, Woodworth and many others. According to this theory, wings are derived from thoracic tracheal gills, which have lost their original function and become adapted for purposes of flight. Tracheal gills, however, are very inconstant in position, and may be developed from the dorsal aspect of the terga, from the sterna or the pleura, at the apex of the abdomen, on the head and even between the wings. Furthermore, there is good reason to believe that if the tracheal gill theory were upheld, we should have to conclude that the ancestors of winged insects were temporarily aquatic, and thus acquired gills, which subsequently developed into wings when these animals became air breathers for the second time. (2) The alternative theory has been conveniently termed by Crampton (1916) the *paranotal theory*. It is due to Muller (1873–75), and among the supporters of this view are Korschelt and Heider, Packard, Comstock and Needham, Handlirsch and others. It is maintained that wings arose in the first instance as lateral expansions (paranota) of the thoracic terga—a view which is not

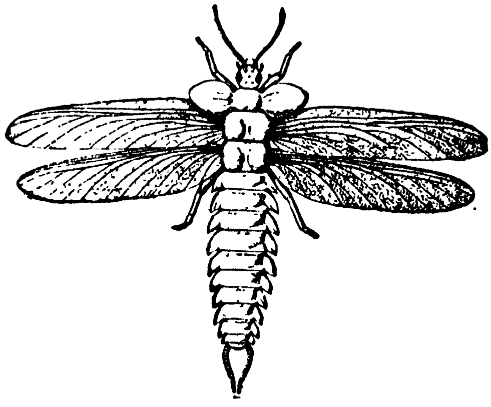

FIG. 38.—A CARBONIFEROUS INSECT (*STENODICTYA LOBATA*) SHOWING PROTHORACIC WING-LIKE EXPANSIONS. From Carpenter, *after* Handlirsch.

inconsistent with the facts of wing development among the lower Pterygota. These expansions are very similar to those found on the prothorax of *Stenodictya* (Fig. 38) and other fossil insects. They are also present on nymphs of *Calotermes* (Fig. 39), and in certain Mantids, Lepismids and Heteroptera, as well as on the abdominal region in various Phasmids. There is, indeed, an inherent tendency towards the development of such structures in diverse groups of insects and in other Arthropods. During the course of their evolution, it is believed that the tergal expansions became sufficiently large to function somewhat after the manner of parachutes, in insects which possessed a tendency to leap. At a later stage, it is claimed, they acquired direct articulation with the tergal region, became supplied with tracheæ and developed the power of independent movement.

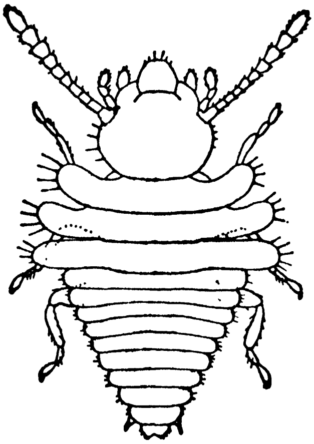
Fig. 39.—A Nymph of *Calotermese dilatatus* showing thoracic wing-like Expansions. *After* Bugnion, *Bull. Mus. d'Hist. Nat.* 1914.

An extended discussion of these, and other theories which have been put forward to account for the origin of insect wings, is given by Woodworth (1906) and Crampton (1916).

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THE ABDOMEN

(*a*) Segmentation of the Abdomen

THE abdomen (Fig. 1) is composed of a series of segments which are more equally developed than in the other regions of the body. For the most part they retain their simple annular form, the terga and sterna are generally undivided shields, while the pleura are membranous and usually without differentiated sclerites. Reduction or special modification of certain of the segments is evident at the anterior as well as at the caudal end of the abdomen, but more especially in the latter region, and this specialization increases from the lower to the higher orders. The abdominal segments are sometimes designated *uromeres* and their primitive number as revealed by embryology is twelve. The last segment or telson is present in the embryos of certain insects (Fig. 40), but it rarely persists: it is evident, however, in the Protura, while in the few cases where it is found in other insects it is vestigial. The 11th segment is present in the adults of the lower orders where its tergum is represented by the *suranal plate* or *epiproct* above the anus (often fused with the 10th tergum), while vestiges of its sternum are seen in the *podical plates* or *paraprocts* which lie on either side of the anus (Fig. 41). The 10th segment is usually distinct and forms the terminal somite in the higher orders. The Protura differ from all other insects in that the number of abdominal segments increases during post-embryonic development, the exceptional number of twelve being present in the adults. The Collembola are also exceptional in possessing never more than six segments, either in the embryo or the adult. In most insects the first abdominal segment, and more especially

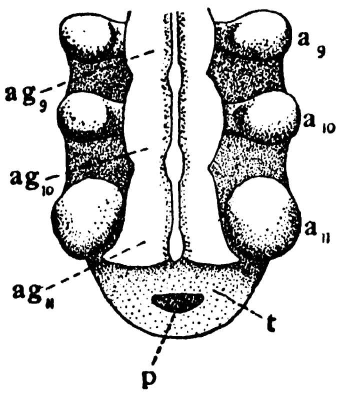

FIG. 40.—VENTRAL VIEW OF LAST ABDOMINAL SEGMENTS OF YOUNG EMBRYO OF *GRYLLOTALPA*. From Heymons.

*a*₉ to *a*₁₁, appendages of 9th to 11th segments and *ag*₉–*ag*₁₁, neuromeres of those segments; *p*, proctodaeum; *t*, telson.

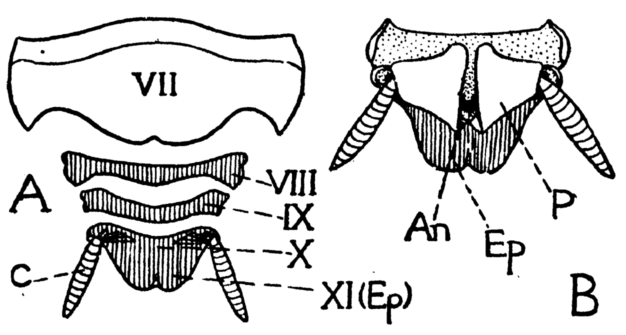

FIG. 41.—LAST ABDOMINAL SEGMENTS OF *BLATTA*. A DORSAL VIEW. B. VENTRAL VIEW.

An, anus; *C*, cercus; *Ep*, epiproct; *P*, podical plate or paraproct VII–XI, terga. *After* Snodgrass.

its sternum, is reduced or vestigial. Among all the Hymenoptera, however, this somite becomes fused with the metathorax during the change from the larva to the pupa and is known as the *propodeum, epinotum*, or *median segment.*

In many insects, more especially certain of those whose eggs are deposited within plant tissues or in other concealed situations, the distal abdominal segments become attenuated and often telescoped, one into the other, to form a retractile tube which is used as an ovipositor. This modification is well exhibited in the Cerambycidæ, Cecidomyidæ, Trypaneidæ, Muscidæ and other families. A true ovipositor is of an appendicular nature and is dealt with in the next section.

(*b*) Appendages and Processes of the Abdomen

In the embryos of most insects evident rudiments of paired abdominal appendages appear at some stage during development. They are commonly present in relation to each segment, excepting the telson (Fig. 40). A variable number of these appendages may become transformed into organs that are functional during post-embryonic life while the remainder disappear. The most conspicuous of such appendages are the *cerci* of the 11th segment, which exhibit wide diversity of form and may even be transformed into forceps, as in the Japygidæ and the earwigs. Among the Apterygota the retention of abdominal appendages is a very general feature. They are well exhibited in the Machilidæ, where they are present in a reduced condition on the 2nd to 9th segments, and as cerci on the 11th segment. These reduced appendages each consist of a limb-base or *coxite* bearing a distal *stylus* which is regarded as the vestige of the shaft of a typical walking limb. In many other Thysanura the coxites fuse with the sterna and the styli arise directly from the composite plates so formed (Fig. 42). For the most part, however, the styli disappear and it is probable that the typical abdominal sternum of insects is a plate of composite origin,—it is, in fact, a "coxosternum." Among the Pterygota abdominal appendages are retained as gills in may-fly nymphs, as abdominal feet in lepidopterous larvæ and as gills in Sialoid larvæ, among Neuroptera. In adult Pterygota the cerci are retained in most of the lower orders and the only other abdominal appendages present are the *gonopods* which enter into the formation of the *genitalia* or external reproductive organs. These are associated with the 8th and 9th segments in the female and with the 9th segment in the male. A completely developed gonopod consists of a coxite bearing a distal stylus, while on its medial border the coxite is produced into a tubular outgrowth or *gonapophysis* (Fig. 43). The genital aperture is usually located in the membrane immediately behind the 8th or 9th segment.

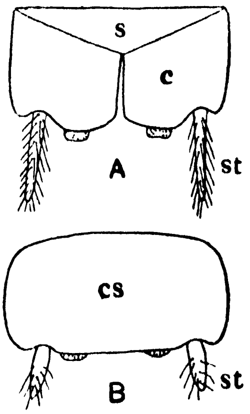

Fig. 42.—Abdominal Sterna and Appendages of A, *Machilis* and B, *Campodea*.

s, sternum; *c*, coxite or limb-base; *cs*, coxosternum; *st*, stylus.

Under the category of abdominal processes are the gills of certain aquatic nymphs and larvæ, the pseudopods of dipterous larvæ, the median caudal filament of Thysanura and Ephemeroptera and the clasping organs of the 2nd abdominal segment of Odonata.

The *female genitalia* consists of three pairs of valves which collectively form the *ovipositor* or egg-laying organ. Their degree of development and co-adaptation varies according to the uses to which that organ is subjected. In the Anoplura, for example, an ovipositor is absent : in *Periplaneta* its valves are very small and free : in the Tettigoniidæ those of one side are held together by tongues and grooves and form, along with their counterparts of the opposite side, an elongate and powerful egg-laying instrument : in most Hymenoptera the ovipositor is greatly attenuated and modified for piercing or stinging. A typical ovipositor is formed by (1) a pair of ventral (anterior) valves representing the gonapophyses of the 8th segment : (2) a pair of inner (posterior) valves formed by the gonapophyses of the 9th segment : and (3) a pair of dorsal (lateral) valves formed by the greatly drawn out coxites of the 9th segment (Fig. 45). It is customary and convenient to refer to all three pairs of valves as gonapophyses, but it will be noted that the dorsal pair alone is homologous with true limbs. In *Machilis* the gonopods are complete but the coxites and styli do not enter into the composition of the ovipositor—the latter being formed by the gonapophyses only (Fig. 44). In the Pterygota the reduced coxites of the 8th segment are transformed into supporting bases for the ventral valves and their styli are wanting. The styli of the 9th segment are almost always absent except in the Odonata, where they are borne at the apices of the dorsal valves. The methods by which the valves of the ovipositor are interlocked are shown in Fig. 46. In Orthoptera the eggs are passed down the combined channel

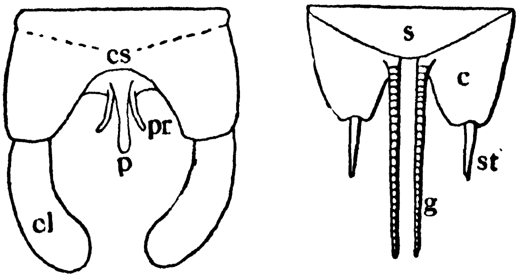

FIG. 43.—LEFT : DIAGRAM OF TYPICAL MALE GENITALIA. RIGHT : A PAIR OF PRIMITIVE GONOPODS.

c, coxite ; *cl*, clasper ; *cs*, coxosternum ; *g*, gonapophysis ; *p*, penis ; *pr*, paramere ; *s*, sternum ; *st*, stylus.

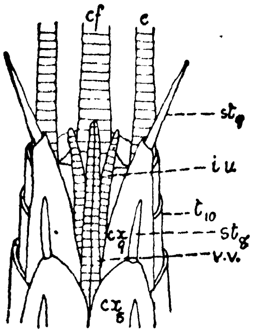

FIG. 44.—VENTRAL VIEW OF THE APEX OF THE ABDOMEN OF A FEMALE *MACHILIS* SHOWING GENITALIA.

c, cercus ; *cf*, median caudal filament ; cx_8, cx_9, coxites of 8th and 9th sterna ; st_8, st_9, styli ; *iv*, *vv*, inner and ventral valves of ovipositor ; t_{10}, 30th tergum. *After* Walker, *Ann. Ent. Soc. Am.* 15.

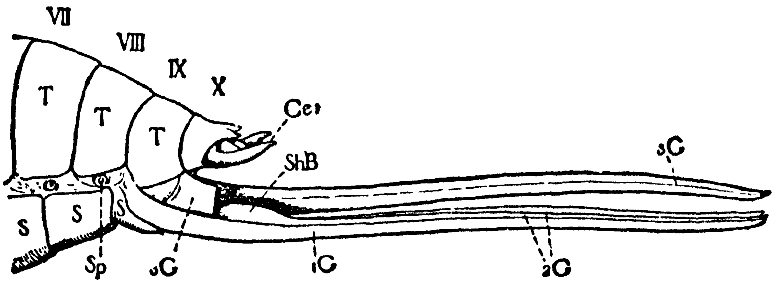

FIG. 45.—OVIPOSITOR OF A LONG-HORNED GRASSHOPPER (*CONOCEPHALUS*).

VII—X, terga ; *s*, *s*, sterna ; *Cer*, cerci ; 1*G*, ventral valve ; 2*G*, inner valves ; ShB, bulb-like swelling formed by the fusion of the bases of 2G ; 3G, dorsal valves, the left one is shown as if cut off near its base. *After* Snodgrass, *U.S. Bur. Ent. Tech. Ser.* 18.

formed by the inner and ventral valves: in most Hymenoptera the inner valves are fused to form a support to the stylets or ventral valves of the sting.

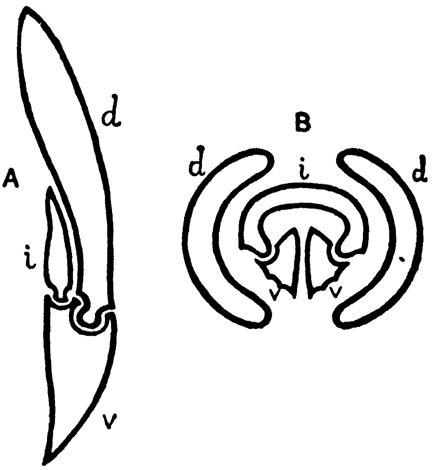

Fig. 46.—Transverse Sections of the Ovipositor of—A, An Orthopteron (*Phasgonura*) *after* Dewitz; B, A Hymenopteron (*Sirex*) *after* Taschenberg. The method of interlocking of the valves is shown.

d, dorsal valve; *i*, inner valve; *v*, ventral valve.

The *male genitalia* (Fig. 43) consist of a pair of gonopods belonging to the 9th segment. The most conspicuous organs are the *claspers* which function in holding the female during coition. These organs are usually regarded as being derived from the coxites of their segment, but the balance of evidence suggests that they are modified styli as claimed by Crampton (1920) and by Snodgrass (1931). While the coxites are distinct, and form the bases of the claspers in may-flies, in most insects they are apparently merged with the 9th sternum. The claspers exhibit great variety of form and structure and are usually composed of a single segment, but in the may-flies (Fig. 47, B) they are several jointed and in Mecoptera and saw-flies they are composed of proximal and distal pieces. Among the Orthoptera and Isoptera the claspers are represented by unmodified styli. What appear to be true gonapophyses are paired outgrowths forming the intromittant organ. In those orders where the growth of these parts has been studied each primary gonapophysis divides. The inner lobes thus developed unite to form the *penis*, while the outer lobes form two small valves or *parameres*: the composite organ thus constituted is termed the *ædeagus*. In a few Dermaptera and among Ephemeroptera the penis retains its original paired condition, but in other insects the fusion is complete. The parameres are well seen in the lower orders (Fig. 47, A), while in the higher groups they are closely merged with the penis, or may be undeveloped as in some Coleoptera. In addition to the foregoing organs, various and often highly complex accessory copulatory structures are present in different orders: they are either developments of the parts just named or special formations.

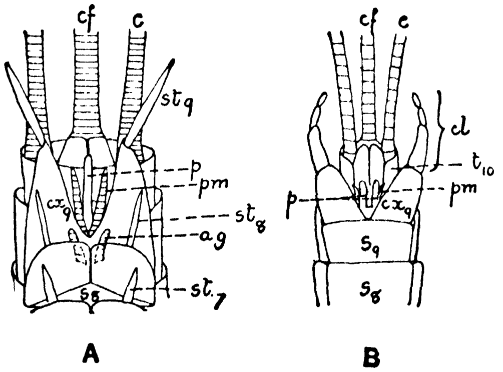

Fig. 47.—Ventral View of the Apex of the Abdomen of A, *Machilis* and B, an Ephemerid showing Male Genitalia.

a.g, accessory genitalia (of 8th segment); *c*, cercus; *cf*, median caudal filament; *cl*, clasper; *cx_9*, coxite of 9th sternum; *p*, ædeagus (paired in B); *pm*, paramere; s_8, s_9, 8th and 9th sterna; st_7–st_9, 7th to 9th styli; t_{10}, 10th tergum. *After* Walker, *Ann. Ent. Soc. Am.* 15.

The morphology of the genitalia in the two sexes is a problem of outstanding difficulty and has been discussed by many writers. According to Verhoeff (1903) the gonopod is a true biramous limb whose coxite represents the protopodite while the stylus and gonapophysis are homologous with an exopodite and endopodite respectively. It is more generally maintained that the coxite and its stylus represent a modified limb, while the gonapophysis is a secondary outgrowth from its base.

The male genitalia are not readily homologized with those of the female. Excepting the anterior parameres of certain Machilidæ (p. 218) the 8th segment bears no counterparts of the ventral valves of the ovipositor. The claspers of the 9th segment are not strictly homologous with the dorsal valves of the ovipositor since they appear to be modified styli, whereas the ovipositor valves are elongated coxites. If the inner valves of the ovipositor have their homologues in the male the combined penis and parameres would appear to be their representatives.

General Literature on the Abdomen and Genitalia

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THE ENDOSKELETON

IN certain regions of the body the integument becomes invaginated and greatly hardened, forming rigid processes which serve for the attachment of muscles and the support of certain other organs. This internal framework is termed the *endoskeleton* and its individual parts are known as *apodemes*. The latter arise as invaginations of the body-wall between adjacent sclerites, or at the edge of a sclerite or segment. In some insects the mouths of the invaginations persist throughout life but, more usually, the latter become completely solid through the deposition of chitinous material.

The endoskeleton is divisible into (*a*) the tentorium and (*b*) the endothorax.

(*a*) The Tentorium (Figs. 48, 49)

This name is given to the endoskeleton of the head and, in generalized insects, it is composed of two or three pairs of apodemes which coalesce at their bases. The functions of the tentorium are—(1) to afford a basis for the attachment of many of the cephalic muscles and, at the same time, to give rigidity to the head; (2) to lend support to the brain and fore-intestine; (3) to strengthen the points of articulation of certain of the mouth-parts. The apodemes which enter into the formation of the cephalic endoskeleton are termed the *anterior, posterior* and *dorsal arms of the tentorium* according to their positions. The inner ends of these arms fuse with those of the opposite side of the head and the median skeletal part, thus formed, is termed the *body of the tentorium*

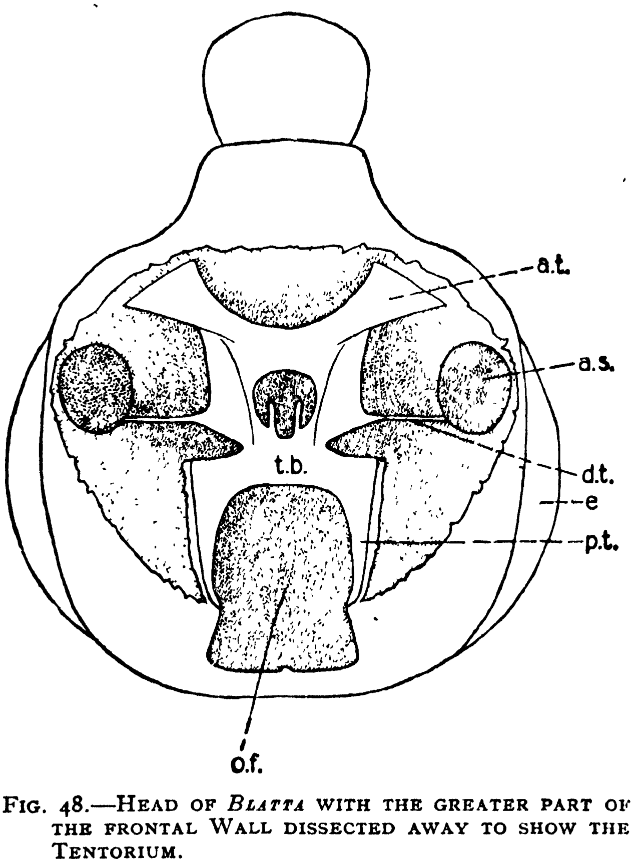

Fig. 48.—Head of *Blatta* with the greater part of the frontal Wall dissected away to show the Tentorium.

as, antennal socket; *at, dt, pt*, anterior, dorsal and posterior arms of tentorium; *e*, compound eye; *of*, occipital foramen *tb* body of tentorium.

The anterior arms of the tentorium.—The invaginations which form these apodemes usually lie on either side of the clypo-frontal suture, when the latter is present, and just above the condylar articulations for the mandibles. While in most insects they are manifested externally as mere pits, in many Diptera they are in the form of intra-cranial tunnels.

The **posterior arms of the tentorium.**—These apodemes are derived from ingrowths situated at the ventral ends of the postoccipital sutures and generally in close relation with the occipital foramen. In some prognathous types they tend to lie more forward on the ventral wall of the head (vide p. 17).

The **dorsal arms of the tentorium.**—These arise not as integumental invaginations but as outgrowths either from the body of the tentorium, or from the bases of the anterior arms. They pass upwards and outwards often to become attached to the head wall near the antennal or ocular sclerites. They are generally present in Orthoptera, but in some cases (e.g. *Blatta*) they are tendon-like, while they are often undeveloped in other orders.

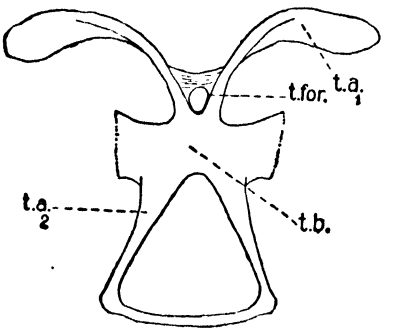

FIG. 49.—TENTORIUM OF A WINGED TERMITE.

ta_1, *ta_2*, anterior and posterior arms; *tb*, body of tentorium; *t for.*, tentorial foramen.

The **body of the tentorium.**—This is a median plate which is often large and its shape varies to some extent in conformity with that of the head: thus, in the soldiers of many termites it is elongate, while in the workers it is a relatively narrow band.

(*b*) The Endothorax (Figs. 50, 51)

Under the term endothorax is included the endoskeleton of the thorax. It is composed of invaginations of the tergal, pleural and sternal regions of a segment and these several apodemes may be conveniently termed the *endotergites*, the *endopleurites* and the *endosternites* respectively.

The **endotergites or phragmas** arise as transverse infoldings between adjacent tergites. Their main function is to provide increased attachment for the longitudinal tergal muscles, and they are principally developed in winged insects. The phragmas arise differently in different insects according to whether the postnotum is present or not and, furthermore, they may be attached either to the hind margin of a tergite, or to the frontal margin of the sclerite immediately behind. In cases where the postnotum is wanting, the phragma is developed in relation with the notum and is termed a *prephragma.* When the postnotum is also present the phragma developed in relation with it is termed the *postphragma.* Both a pre- and post-phragma may be carried by either the meso- or meta-thorax in some orders of insects,

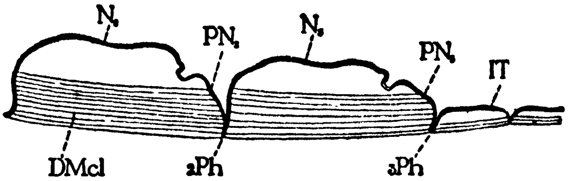

FIG. 50.—LONGITUDINAL SECTION THROUGH THE BACK OF THE MESO- AND META-THORAX AND BASE OF THE ABDOMEN OF A STONEFLY (*ALLOPERLA*).

D.M.cl, dorsal longitudinal muscles. IT, 1st abdominal tergum N_2, mesonotum; N_3, metanotum; PN_2, PN_3, postnotum of meso- and meta-thorax; 2Ph, 3Ph, phragmas. *After* Snodgrass, *Proc. U.S. Nat. Mus.* 39.

but no phragma is ever borne by the prothorax. These apodemes commonly lie between adjacent segments and, consequently, an individual phragma is regarded as belonging to the segment behind it. Three phragmas are usually present, the first being situated between the pro- and meso-terga, and the third between the meta-tergum and the first abdominal tergum. For a discussion of the morphology of these apodemes vide Snodgrass (1929),

The **endopleurites** or **lateral apodemes** are infoldings between the pleurites. In a typical wing-bearing segment of most insects there is a single apodeme on either side and it is known as the *pleural ridge.* The latter terminates in the wing process above, the coxal process below, and often bears an inwardly projecting *pleural arm.* The endopleurites are well developed in the Odonata where, according to Berlese, there are five pairs. In *Melanoplus* the mouths of the primitive invaginations remain open in the adult insects (Comstock).

The **endosternites** (**apophyses** of some writers) are commonly represented by the *furcæ*; each furca is a median apodeme, unpaired at its base, with two free distal arms. In many Orthoptera, for example, there is also a median unbranched apodeme or *spina* which lies behind the furca. In the Odonata the endosternites are paired, and are inclined so far inwards, towards the median line, that they almost meet over the nerve cord. In the honey bee those of the prothorax fuse to form a supraneural bridge, and the combined meso- and meta-thoracic endosternites together form a second bridge of a similar character.

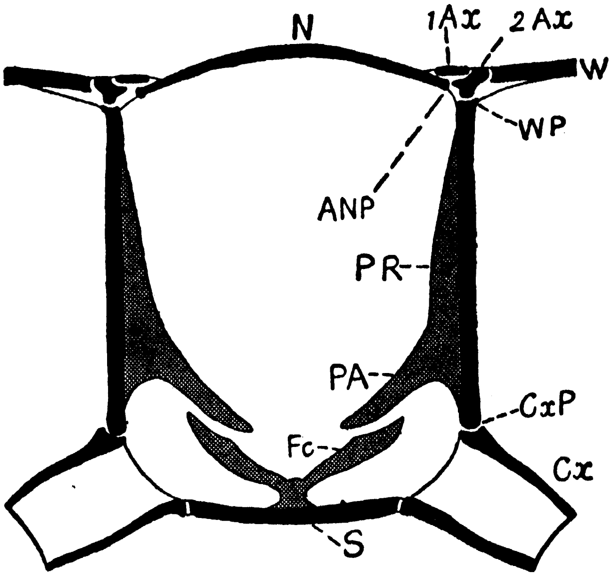

FIG. 51.—DIAGRAM OF A SECTION ACROSS A WING-BEARING SEGMENT.

ANP, anterior notal wing process; *1Ax*, *2Ax*, 1st and 2nd axillary sclerites; *Cx*, coxa; *CxP*, coxal process of pleuron; *Fc*, furca; *N*, notum; *PA*, pleural arm; *PR*, pleural ridge; *S*, sternum; *W*, wing; *WP*, wing process of pleuron. *After* Snodgrass, *Proc. U.S. Nat. Mus.* 36.

(*c*) The Abdominal Endoskeleton

In the abdomen apodemes are developed for the purposes of giving firm bases of origin to certain of the more important muscles. Most of the terga usually present internal ridges or phragmas, as in the thorax, giving attachment to the chief longitudinal muscles. On the ventral aspect sternal apophyses, in connection with the protractor and dilator muscles, are commonly present and in some cases highly developed.

Literature on the Endoskeleton.—There is little special literature dealing with the endoskeleton. Reference should be made to the more general papers listed under the sections dealing with the three main regions of the body.

THE MUSCULAR SYSTEM

THE muscles of insects are, for the most part, translucent and either colourless or grey, but the wing muscles frequently exhibit a yellow, orange, or brown tinge. Unlike vertebrate muscles, the fibres of both the voluntary and involuntary muscles of insects are cross-striated, the striæ being generally very conspicuous and easily seen. Insect muscles also differ fundamentally from those of the Annelida not only in histological structure, but also in the fact that they are never incorporated with the layers of the body-wall to form a dermo-muscular tube.

In the case of most of the voluntary muscles, and those of the appendages in particular, one of the extremities of a muscle is attached to a relatively stationary skeletal part and the other is attached to the region or organ which is movable. The attachment to the stationary base is the *origin* and that to the movable part is the *insertion* of the muscle. In many instances the fibres of a muscle are directly fixed into the parts which serve as the origin and insertion. In others chitinous cords, bands, or integumentary invaginations known as *tendons* intervene between the points of attachment and the actual muscle as, for example, in the muscles of the mandibles.

(*a*) Histology of the Muscles (Figs. 52, 53)

As already mentioned, the muscle fibres of insects are prominently striated and, in those of the leg and other parts, the striæ are clearly visible in the living untreated tissue. In suitably stained preparations the striæ are observable throughout the muscles of the body, including those of the alimentary canal, and the delicate fibres in the walls of the heart. Each fibre consists of a number of highly elastic longitudinal fibrillæ or *sarcostyles* which are composed of alternate light (isotropic) and dark (anisotropic) portions. By the juxtaposition of the light and dark zones in adjacent fibrils the familiar banded or cross-striated appearance of muscle is produced (Fig. 52). In the middle of each clear band or zone is a transverse septum termed *Krause's membrane* to which the sarcostyles are joined. This membrane is composed of a network of radially distributed threads, which cut across the muscle fibre, thus dividing it into short lengths or *sarcomeres*. A muscle fibre may be regarded as a greatly attenuated multinucleate cell which is bounded by a delicate coat or *sarcolemma*. The

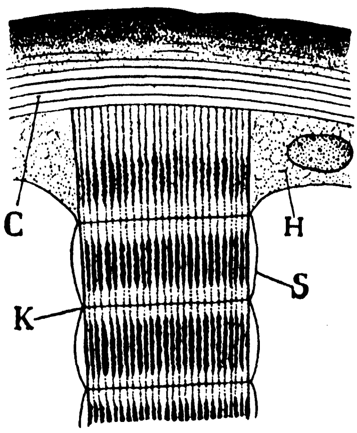

FIG. 52.—THORACIC MUSCLE FIBRE OF BEE.

C, cuticle; *H*, hypodermis; *K*, Krause's Membrane (telophragma); *S*, sarcolemma. Adapted from Morison.

fibre contains a certain amount of undifferentiated protoplasm or *sarcoplasm* in which the sarcostyles are embedded. When a nerve-impulse is received the component fibres of a muscle shorten, the process being attributed to the shortening of the dark bands of the individual sarcostyles. The contraction of the muscle as a whole results in the movement of the part or organ concerned. When the stimulus ceases the radial fibres, by their elasticity, are believed to bring the sarcostyles back into the position assumed when relaxed. Several types of muscle fibres are found among different insects (Fig. 53). Thus, in many larvæ and among Apterygota the sarcostyles are surrounded by a thick layer of sarcoplasm containing the nuclei. This same general type of fibre is present in the leg and abdominal muscles of beetles and other insects, only the sarcoplasm is greatly reduced and the sarcostyles are usually more numerous. Among adult Hymenoptera and Diptera the fibres are tubular in character with the sarcostyles disposed radially around a central core of sarcoplasm in which are embedded the nuclei. The indirect wing muscles of the bee and other insects have exceptionally large fibres which are readily separated apart and the sarcolemma is usually wanting, while the nuclei are either peripheral or embedded in the body of the fibre. Such fibres have a rich tracheal supply and lying in regular rows between the sarcostyles are deeply-staining bodies or sarcosomes whose significance is obscure.

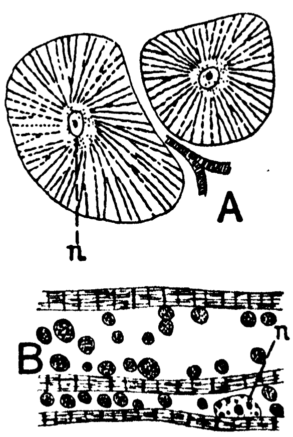

Fig. 53.—Muscle Structure.

A, transverse section of two sarcostyles of a leg-muscle fibre of a bee. Original. B, sarcostyles with sarcosomes from a wing-muscle of *Hydrophilus*. *After* Schneider. *n*, nucleus. Highly magnified.

The involuntary muscles of insects exhibit a totally different structure from those of vertebrates and, in their striated appearance and frequent tendency to branching, they bear a resemblance to cardiac muscle. The detailed structure of insect muscle and its interpretation are dealt with in appropriate textbooks, and reference should also be made to original papers by Janet (1895), Jordan (1919–20) and Morison (1927).

The actual nature of the attachment of muscles to the cuticle has been much discussed. In the majority of cases a zone of non-striated fibrils intervenes between the contractile substance of a muscle and its point of attachment. Snethlage (1905), Holmgren (1910), and Jordan (1919) claim that such fibrillæ are prolongations of the muscle itself and consequently the latter is attached directly to the cuticle. Henneguy (1906), who gave the name *tonofibrillæ* to these fibrils, and more recent observers, state that they are of a cuticular nature, being derived from the substance of the intervening hypodermis. Since the muscles are mesodermal tissues it follows, on this theory, that the outer ends of the sarcostyles become secondarily attached to the cuticle by means of tonofibrillæ.

(*b*) Arrangement of the Muscles (Myology) (Figs. 54, 55)

In general arrangement the muscular system corresponds with the segmentation of the body and is exhibited in its least modified condition in the Apterygota, the lower Pterygota and in many larvæ. The number of muscles is very great: in a lepidopterous larva there are about 2000, and in the imagines of several orders the number is correspondingly increased owing to the development of wings. With few exceptions, the somatic muscles are paired, thereby conforming to the general bilateral symmetry of the body, and the names of the muscles generally indicate the origins and insertions, or the functions, of the latter. The splanchnic muscles, on the other hand, usually exhibit no such symmetry and, as they do not come under the general category of myology, they are dealt with in the sections devoted to the different internal organs.

Although detailed studies of the musculature of several types of insects are available, the homologies of the various muscles are often difficult to determine and no uniform terminology has been evoked. The points of attachment of apparently homologous muscles also vary to some extent in different insects, and the subject of comparative myology is not sufficiently advanced for general treatment. The principal muscles of an orthopterous insect, taken as the type among the lower insects, are enumerated below, but to deal adequately with all those present would encroach upon more space than is available and demand a wealth of illustration. On account of the musculature exhibiting its most generalized condition in the abdomen, the myology of this region will be considered first and the cephalic muscles last.

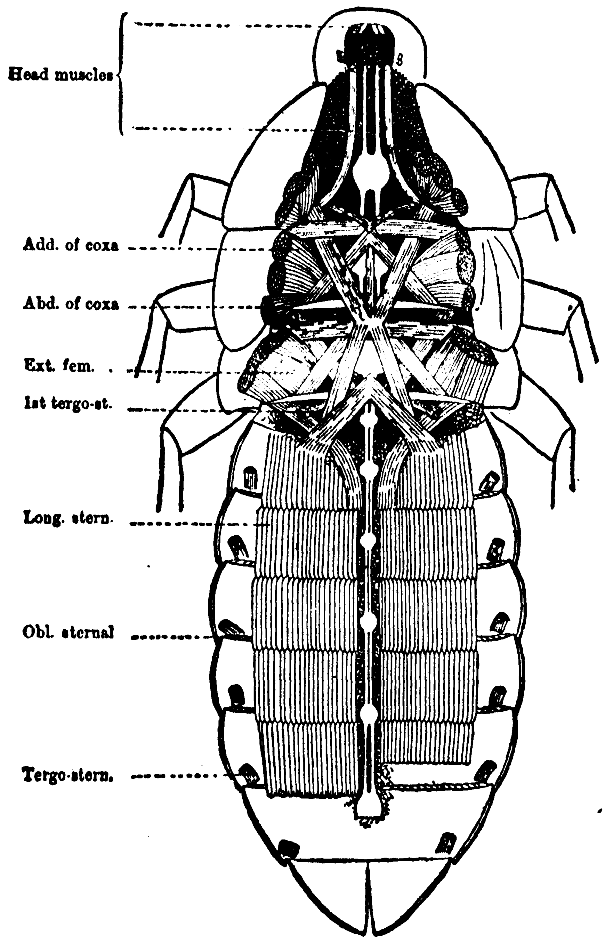

Fig. 54.—Muscles of the Ventral Wall of a Cockroach, with the Nerve Cord. *After* Miall and Denny.

A. The **Abdominal Muscles**.—The principal muscles of a typical abdominal segment may be grouped into the following series.

1. LONGITUDINAL. These are divisible into *tergal* and *sternal muscles.* They arise from the tergum or sternum, as the case may be, and are inserted into the corresponding region of the segment behind. They function as retractors of the abdomen and the two groups, working together, telescope the abdomen. Acting alone, the sternal muscles curve the abdomen downwards and the tergal muscles straighten it or bend it upwards.

2. DORSO-VENTRAL. This series consists of the *tergo-sternal muscles*; they arise from the tergum of their segment and, passing downwards, are inserted into the sternum. Along with most of the pleural muscles, they bring about the expiratory process by approximating the tergum and sternum thereby compressing the segment.

3. PLEURAL. These consist of *sterno-pleural* and *noto-pleural muscles.* The former originate from the sternum and are inserted on the pleura or the spiracles: the latter muscles arise from the tergum and are likewise inserted into the pleura.

In addition to the above, there are also special muscles concerned with the movements of the genitalia and cerci.

B. The **Thoracic Muscles**.—The chief groups of muscles of a wing-bearing segment are as follows.

1. LONGITUDINAL. As in the abdomen these are divisible into *tergal* and *sternal muscles*.

2. DORSO-VENTRAL. These are divisible into *tergo-sternal* and *noto-pedal muscles*. The latter take their origin from the tergum and are inserted into the bases of the legs: they are divided by Berlese into noto-subcoxal, noto-coxal and noto-trochanteric muscles, according to the positions of their insertions. They principally function as extensors and flexors of the coxæ and extensors of the femora.

3. PLEURAL. Of these muscles there are four groups, viz., the *pleuro-pedal*, *noto-pleural*, *sterno-pleural* and *sterno-pedal* muscles. They are concerned with the movements of the coxæ and femora, with the elevation and depression of the tergum, thereby raising or lowering the wings, and with the compression of the pleura.

4. THE LEG-MUSCLES. In addition to the noto-pedal and certain of the pleural muscles, which are concerned with the movements of the legs as a whole, there are also a number of muscles which lie within the joints of the legs. These latter include the flexors and extensors of the femora, tibiæ and tarsi and the flexors of the claws.

C. **Cephalic Muscles**.—The principal muscles of the head may be divided into (*a*) cervical muscles, (*b*) muscles of the mouth-parts, and (*c*) muscles of the antennæ.

(*a*) The CERVICAL MUSCLES.—These control the movements of the head and are classified into levators, depressors, retractors, and rotators according to their function. They take their origin from the prothorax and cervicum and are inserted into the tentorium and epicranium.

(*b*) The MUSCLES OF THE MOUTH-PARTS.—Associated with the labrum are two pairs of muscles:—

1. The *levators*. A pair of contiguous muscles originating in the middle of the frons and becoming inserted into the base of the labrum.

2. The *depressors*. These muscles arise on the head capsule and are inserted into the base of the labrum on either side of the levators.

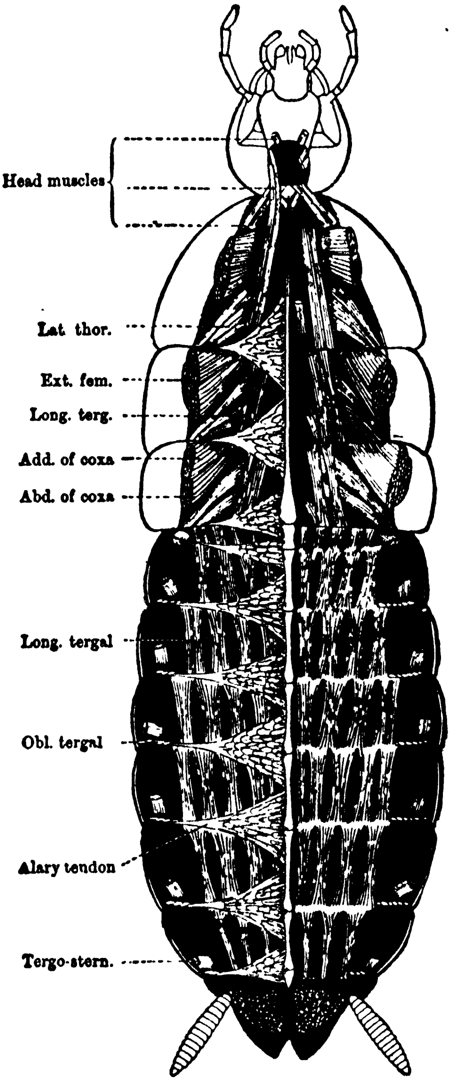

FIG. 55.—MUSCLES OF THE DORSAL WALL OF A COCKROACH, WITH THE HEART AND PERICARDIAL TENDONS. *After* Miall and Denny.

The mandibular muscles consist of—

3. The *adductor* (flexor). This large muscle has an extensive origin on the roof and back of the head, and is inserted, by means of a plate-like tendon, into the inner angle of the base of the mandible. In many insects a second or short adductor is also present.

4. The *abductor* (extensor). The origin of this muscle is on the upper lateral portion of the epicranium and its tendonous insertion is on the outer basal angle of the mandible.

The principal maxillary muscles are as follows—

5. The *adductors*. These form a large group of three muscles which take their

origin from the lower surface of the central plate of the tentorium, and are inserted into the cardo and the base of the stipes.

6. The *abductor.* This muscle originates from the posterior region of the epicranium near the abductor of the mandible and is inserted into the cardo.

7. The *adductor of the galea.* A muscle which originates from the base of the stipes and has its insertion in the inner angle of the base of the galea.

8. The *adductor of the lacinia.* This muscle arises near to the attachment of the previous muscle and is inserted into the inner basal angle of the lacinia.

9 and 10. The *flexor and extensor of the palpus.* Both these muscles arise within the stipes and are attached respectively into the inner and outer sides of the base of the palpus. The joints of the palpus are also movable by means of separate muscles.

The muscles of the labium (Fig. 13) are—

11. The *lateral retractors.* A pair of elongate muscles arising from the posterior arms of the tentorium and inserted near the bases of the paraglossæ.

12. The *median retractors.* Two contiguous muscles arising from near the middle of the submentum or postmentum, as the case may be, and inserted into the base of the prementum.

13. The *distal retractors.* A pair of muscles arising from the posterior arms of the tentorium and inserted near the inner bases of the glossæ.

14. The *flexors of the paraglossæ.* These arise from the base of the prementum and are inserted in the bases of the paraglossæ.

15. The *flexors of the glossæ.* Similar in origin to 14 and inserted into the bases of the glossæ.

16. The *abductors of the palpi.* These arise from the palpigers and are inserted into the bases of the palpi.

17. The *adductors of the palpi.* Transverse muscles arising from the median apodeme between the glossæ and passing outwards to the bases of the palpi.

There is also an extensor muscle of the 2nd palpal segment and a flexor of the 3rd segment. In association with the hypopharynx are protractor and retractor muscles and dilator muscles in connection with the salivary orifice.

(*c*) The MUSCLES OF THE ANTENNÆ :

1. The *levators.*
2. The *depressors.*

These muscles arise from the anterior and dorsal arms of the tentorium, or from the dorsal arms only : they are attached to the bases of the scape. There are usually two pairs of depressors.

3. The *extensors of the flagellum.* Arising near the insertion of 1 and attached to the dorsal margin of the base of the pedicel.

4. *The flexor of the flagellum.* Arising from the base of the scape and inserted into the base of the pedicel.

D. **Muscles of Flight.**—The flight of insects has been alluded to on p. 42, and the mechanism of the process has been studied by Ritter (*Smithsonian Misc. Coll.*, 56, 1912) in *Calliphora,* Stellwaag (1910), in the bee and by others. The flight movements are effected by two sets of muscles—*indirect muscles* and *direct muscles* (Figs. 56, 57).

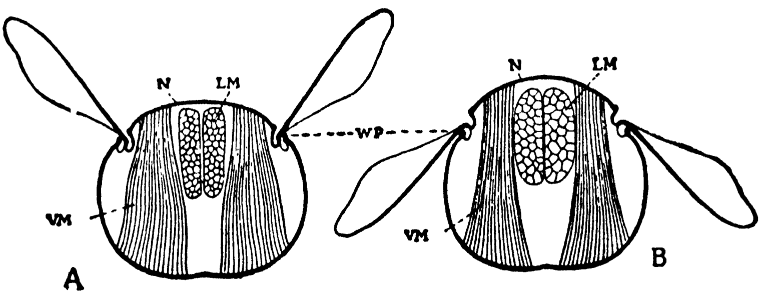

FIG. 56.—DIAGRAMMATIC CROSS-SECTION OF THORAX OF A BEE THROUGH PLEURAL WING PROCESS *WP.*

A, wings thrown upward by depression of tergum *N* caused by contraction of vertical muscles *VM*. B, wings thrown downward by elevation of tergum *N* caused by contraction of longitudinal muscles *LM*. *After* Snodgrass.

The *indirect muscles* are the largest in the body, and are attached to the thorax and not to the wing-bases. In the hive bee they consist of two groups of muscles : (1) a pair of dorso-ventral muscles by whose contraction the tergal region of the thorax is depressed, with the result that the wings are forced upwards owing to the peculiar nature of their articulation with the thorax; (2) a pair of longitudinal muscles by whose contraction the tergal region becomes arched upwards which results in the wings being forced downwards. The rapid alternate contraction of these two groups of muscles consequently raises and lowers the wings by their action upon the dorsal wall of the thorax. The *direct muscles* (Fig. 57) are pleural muscles and consist typically of four pairs—(*a*) the 1st anterior extensor arising usually from the sternal region and attached to the basalar sclerite (p. 34); (*b*) the 2nd anterior extensor arising from the rim of the coxa, just in front of its pleural articulation, and similarly inserted into the basalar sclerite; (*c*) the posterior extensor arising from the rim of the coxa, just behind its pleural articulation, and inserted into the subalar sclerite; (*d*) the flexor arising from the pleural ridge and inserted into the 3rd axillary sclerite. While the indirect muscles are alternately elevating and depressing the wings, the forward and backward movements of the latter are effected by muscles (*a*), (*b*) and (*c*), while muscle (*c*) also aids in depressing the wing. These same muscles, furthermore, bring about the turning of the wing on its long axis. The complete mechanics of the wing during flight is a complex process. During the downstroke the wing is pulled downwards and forwards while its anterior margin is deflected and its posterior area upraised. During the upstroke the wing is pulled upwards and backwards while the posterior area, at the same time, is deflected. The flexor muscle is concerned with whatever folding the wing undergoes during flexion and in drawing the wing towards the side of the body.

In the Odonata, Lendenfeld (1881) has shown that the usual indirect muscles are wanting, and flight is effected solely by direct muscles of which there are eight to each wing.

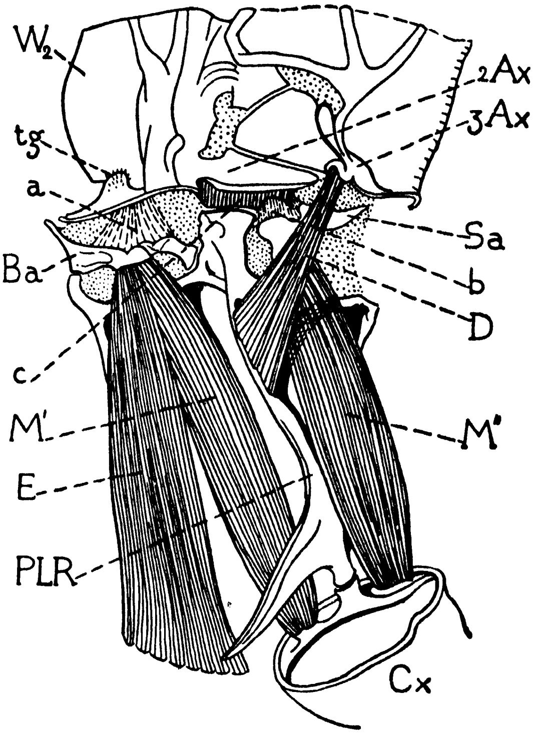

FIG. 57.—DIRECT WING MUSCLES OF MESOTHORAX OF A GRASSHOPPER.

2 *Ax*, 2nd axillary sclerite and *c*, its ventral plate; 3 *Ax*, 3rd axillary sclerite; *Ba*, basalar sclerites; *Cx*, coxa; *D*, flexor muscle; *E*, 1st anterior extensor muscle; *M'*, 2nd anterior extensor muscle; *M''*, posterior extensor muscle; *PLR*, pleural ridge; *Sa*, subalar sclerite; *tg*, tegula; W_2, fore-wing, turned upward. Adapted from Snodgrass, 1930.

Descriptions of the musculature are to be found in the following works: Lyonnet on the larva of *Cossus*; Straus-Durckheim on *Melolontha*; in Newport's article "Insecta"; Kunckel d'Herculais on *Volucella*; Hewitt on *Musca*; Miall and Denny on *Periplaneta*; Tillyard on the *Odonata*; and Berlese on the *Protura*. In addition to the above, special studies of the musculature are listed below.

Literature on the Muscles

BAUER, 1910.–Die Muskulatur von *Dytiscus marginalis*. *Zeits. wiss. Zool.* 95. **DIRKES, 1928.**–Das larvale Muskelsystem und die Entwicklung der imaginalen Flugmuskulatur von Psychoda. *Zeits. Morph. Ökol. Tiere,* 11. **DU PORTE, 1920.**–The Muscular System of *Gryllus domesticus* Fabr. *Ann. Ent. Soc. Am.* 13. **FORBES, 1914.**–A Structural Study of the Caterpillars, III. The Somatic Muscles. *Ann. Ent. Soc. Am.* 7. **FORD, 1925.**–A Comparative Study of the Abdominal Musculature of Orthopteroid Insects. *Trans. Roy. Soc. Canad. Inst.* 14. **VAN GEHUCHTEN, 1886.**–Étude sur la structure intime de la cellule musculaire striée. *La Cellule* 2. **HENNEGUY, 1906.**–Les modes d'insertion des muscles sur la cuticle chez les Anthropodes. *C. R. Assoc. Anat.* 8. **HOLMGREN, 1910.**–Uber die Muskelinsertionen an das Chitin bei den Arthropoden. *Anat. Anz.* 36. **HURTHLE, 1909.**–Ueber die Struktur der quergestreiften Muskelfasern von *Hydrophilus*, etc. *Arch. gen. Physiol.* 126. **JANET, 1895.**–Structure des Membranes, Articulaires des Tendons et des Muscles. (Études sur les Fourmis, etc., 12th Note.) Limoges. **JORDAN, 1919–20.** –Studies on Striped Muscle Structure. *Anat. Record,* 16 and 19; *Amer. Journ. Anat.* 27. **LUBBOCK, 1858.**–On the Arrangement of the Cutaneous Muscles of the Larva of *Pygæra bucephala. Trans. Linn. Soc.* 22. **MORISON, 1927–28.**–The Muscles of the Adult Honey-bee. *Quart. Journ. Mic. Sci.* 71, 72. **PETRI, 1899.**–I. Muscoli delle ali nei ditteri e negli imenotteri. *Bull. Soc. Ent. Ital.* 31. **PLATEAU, 1865–66.** –Sur la force musculaire des Insectes. *Bull. Acad. Roy. Belg.* 2nd ser. 20, 22. —— **1884.**–Recherches sur la force absolue des muscles des Invertébres. *Ibid.* 3rd ser. 6. **SAMTLEBEN, 1929.**–Anatomie u. Histol. der Abdominal und Thoraxmuskulatur von Stechmückenlarven. *Zeits. wiss. Zool.* 134. **SNETHLAGE, 1905.**–Ueber die Frage von Muskelansatz und der Herkunft der Muskulatur bei den Arthropoden. *Zool. Jahrb. Anat.* 21. **SNODGRASS, 1929.**–Vide p. 44. —— **1931.**–Vide p. 50. **SOLF, 1931.**–Reizphysiologische Untersuchungen am Orthopteren Musculatur. *Zool. Jahrb., abt. Allg. Zool.* 50. **VOSS, 1905.**–Ueber die Thorax von *Gryllus domesticus.* II. Die Muskulatur. *Zeits. wiss. Zool.* 78. **WALKER, 1931.**–On the Anatomy of *Grylloblatta.* 1. Exoskeleton and Musculature of the Head. *Ann. Entom. Soc. America,* 24. **WEBER, 1928.**–Skelett, Muskulatur und Darm der *Aphis fabæ. Zoologica,* 28.

See also literature on flight, p. 44.

THE NERVOUS SYSTEM

I. The General Nervous System

THE nervous system of insects may be divided into the central nervous system, the visceral nervous system and the peripheral sensory nervous system.

(*a*) The Central Nervous System

This constitutes the principal division of the nervous system and is composed of a double series of ganglia which are joined together by means of longitudinal and transverse cords or strands of nerve fibres (Fig. 58). The longitudinal cords are termed *connectives* and they serve to join a pair of ganglia with those which precede and succeed it. The transverse fibres or *commissures* unite the two ganglia of a pair. Typically there is a pair of ganglia in each segment of the body, but the members of a pair are usually so closely united that they appear as a single ganglion, the commissure being no longer evident. The connectives are separate and distinct throughout the body as in *Machilis* and *Corydalis*, or in the thorax only as in the Orthoptera, Coleoptera and many lepidopterous larvæ, but usually they are so closely approximated as to appear as a single longitudinal cord. In many cases the ganglia of adjacent segments coalesce to form *ganglionic centres*. Two of the latter are always present in the head, and varying degrees of coalescence of the thoracic and abdominal ganglia are revealed by a comparative study of the nervous system in different orders of insects (vide Brandt, 1879).

Seen in transverse sections, a typical nerve ganglion is invested by a synctytial membrane or epineurium which also forms the covering coat of the principal nerves. Beneath the epineurium are groups of nerve or ganglion cells enclosing a central medullary substance or neurospongium. The ganglion cells are for the most part unipolar and are chiefly evident by their nuclei, the cytoplasm being of relatively small amount. The neurospongium is formed by the

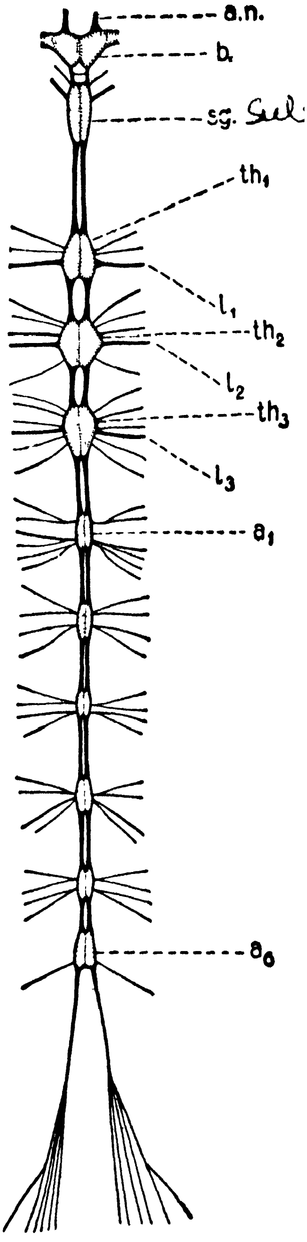

FIG. 58.—CENTRAL NERVOUS SYSTEM OF *FORFICULA*.

a.n, antennary nerve; *b*, brain; *s.g.*, subœsophageal ganglion; th_1–th_3, thoracic ganglia; l_1–l_3, nerves to legs; a_1–a_6, first and terminal abdominal ganglia.

fine twigs of the axons of the ganglion cells which are held together by means of a variable amount of neuroglœa: when viewed in sections the neurospongium presents a punctured appearance owing to the twigs being cut across in large numbers (Viallanes, 1886). The nerve fibres of insects resemble those of the grey or non-myelinated type in vertebrates and each is enclosed in a delicate sheath or neurilemma.

The central nervous system is divisible into the brain or cerebral ganglion, the subœsophageal ganglion and the ventral nerve cord.

1. The **Brain** (Figs. 59–61) lies just above the œsophagus between the supporting apodemes of the tentorium. It is the dorsal ganglionic centre of the head and is formed by the coalescence of the first three neuromeres in the embryo. This threefold division is maintained in the completed organ which is divided into corresponding regions which are designated the *protocerebrum*, the *deutocerebrum* and the *tritocerebrum* respectively. Among the chief writings on the structure of the brain are those of Viallanes (1886–1887), Haller (1905), Janet (1905), and Jonescu (1908).

The PROTOCEREBRUM represents the fused pair of ganglia of the optic segment. It forms the greater part of the brain and innervates the com-

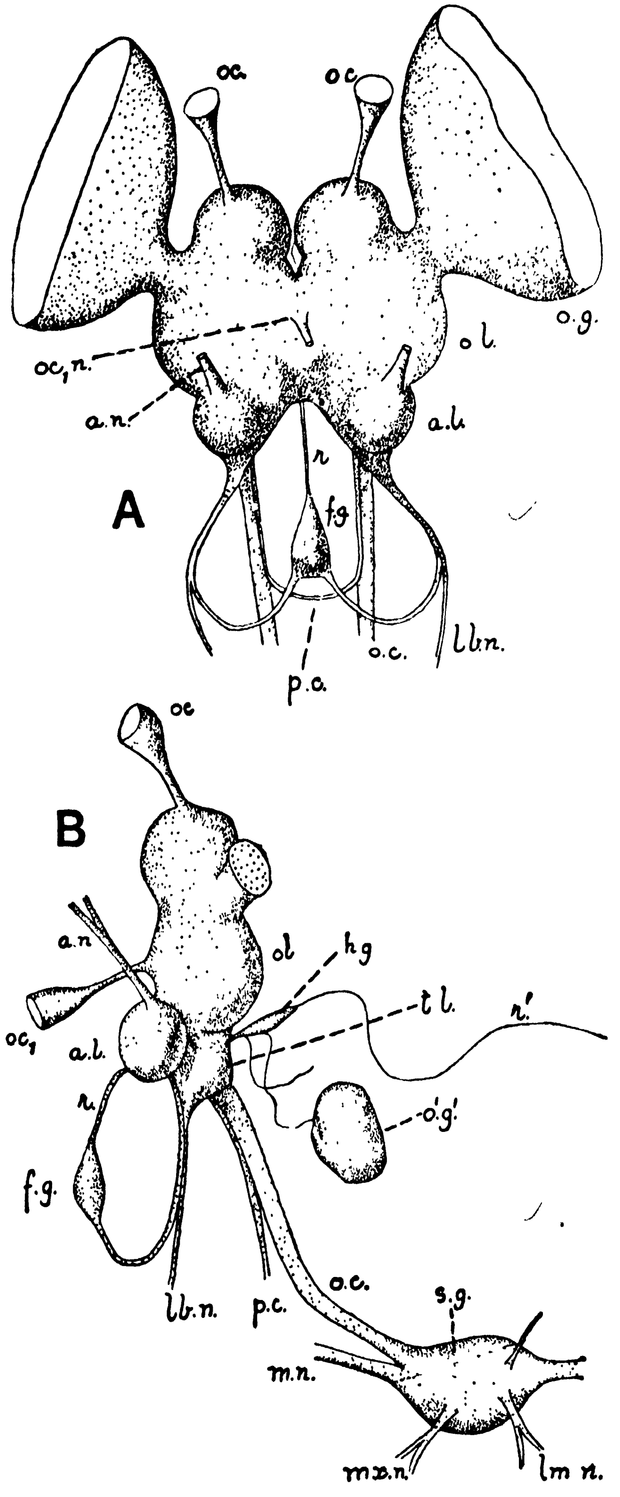

FIG. 59.—BRAIN AND SUBŒSOPHAGEAL GANGLION OF A LOCUST (CALOPTENUS).

A, frontal view; B, lateral view. *a.l*, antennary lobe; *a.n*, antennary nerve; *f.g*, frontal ganglion; *h.g*, hypocerebral ganglion; *lb.n*, labral nerve; *lm.n*, labial nerve; *m.n*, mandibular nerve; *mx.n*, maxillary nerve; *oc*, lateral ocellus; oc_1, median ocellus; oc_1n, root of nerve to median ocellus; *o.c*, para-œsophageal connective; *o.g*, optic ganglion; *o'.g'*, œsophageal ganglion; *o.l*, optic lobe; *p c*, post-œsophageal commissure; *r*, recurrent nerve (continued in B as the stomatogastric nerve r^1); *s.g.*, sub-œsophageal ganglion; *t.l*, tritocerebral lobe. *After* Burgess, *2nd Rep. U.S. Ent. Comm.*

pound eyes and ocelli. The protocerebrum is divisible into (1) the protocerebral lobes, and (2) the optic lobes.

(1) The *protocerebral lobes* are fused together along the median line to form a bi-lobed ganglion. They are composed of a cortex, consisting of an immense number of small ganglion cells, which surround a central core of nerve-fibres constituting the medulla. The two lobes are interconnected by a median commissural system termed the *central body*, towards which fibres converge from various parts of the brain. In addition to the central body there are two smaller commissures, viz. the anterior and posterior dorsal. The *anterior dorsal commissure* (" commissure cérébrale supérieure " of Viallanes) passes in front of and above the central body. The *posterior dorsal commissure* (" pont des lobes protocérébraux " of Viallanes) is a ⊓-shaped fibre-tract lying behind the former commissure. The most conspicuous formations in the protocerebral lobes are the *mushroom* or *stalked bodies* which are regarded by many investigators as the principal motor and psychic centres of the brain. Each mushroom body rests on the surface of the protocerebrum and is divisible into an outer and an inner lobe. These lobes are each formed of a peripheral layer of nerve cells and a central fibrous tract, the latter being deeply indented to form the *calyx*. The fibres are produced downwards to form the stalk and the two stalks of a mushroom body coalesce further inwards, thus giving rise to the main peduncle which is inserted deeply in the medulla. In the region of the brain, between the mushroom bodies, are four small *ocellar lobes* from each of which an *ocellar nerve* takes its origin. The two outer nerves supply the paired ocelli, while the two inner nerves unite just outside the brain to form a single nerve supplying the median ocellus.

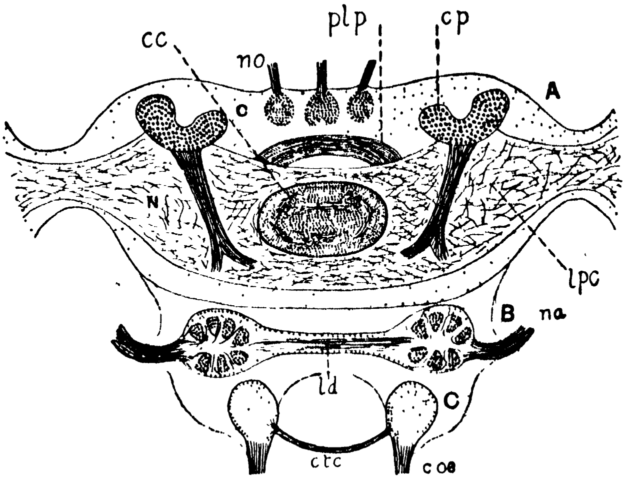

FIG. 60.—GENERALIZED DIAGRAM OF THE THREE PAIRS OF GANGLIA FORMING THE BRAIN.

A, protocerebrum; B, deutocerebrum; C, tritocerebrum. C, cortical (cellular) layer; N, neurospongium. Other lettering as in Fig. 61.

(2) The *optic lobes* (*optic ganglia* or *optic tract*) form the most highly complex region of the brain and their degree of development is in direct relation with that of the compound eyes. Each lobe consists of three principal zones or tracts of nerve tissues which are connected by a similar number of layers of nerve fibres (Figs. 61 and 80). The *ganglionic layer* or *plate* (*periopticon*) is the zone nearest the eye and is connected with the inner ends of the ommatidia (vide p. 80) by the *layer of post-retinal fibres.* The middle zone is termed the *external medullary mass* (*epiopticon*) and is connected with the ganglionic plate by means of the *external chiasma* which is formed by the crossing of nerve fibres. The inner zone is the internal medullary mass (*opticon*), the latter is united with the preceding zone by means of the *internal chiasma.* The nerve fibres of this layer cross completely in a manner similar to those of the external chiasma. The fibres of the *optic nerve* issue from the inner aspect of the internal medullary mass and divide into anterior and posterior bundles, which pass to the centre of the protocerebrum. The whole structure of the optic lobes is extremely complex; their histology is described by Viallanes (1885), and in papers by Hickson and other writers who have investigated the structure of the compound eyes.

The DEUTOCEREBRUM represents the fused ganglia of the antennary segment. It is chiefly composed of the paired *antennary* or *olfactory lobes* which are prominent swellings situated on the antero-ventral aspect of the brain and innervate the antennæ.

The so-called *dorsal lobe* is chiefly represented by a transverse fibrous tract situated above the antennary lobes and serving to connect the latter together. Each half of the dorsal lobe is connected with the protocerebral lobe of the opposite side by means of a chiasma (" cordon chiasmique " of Viallanes) and the antennary lobe is connected with the mushroom body of its side and the central body by the *optico-olfactory chiasma.* Arising from the deutocerebrum are four pairs of nerves as follows: the *antennary nerves* are the longest and most important, and are the sensory nerves of the antennæ; each has two roots, one of which is derived from the antennary lobe of its side and the other from the dorsal lobe. The *accessory antennal nerves* issue from the antennary lobes and are the motor nerves of the appendages concerned. The *tegumentary nerves* are a pair of slender strands arising from the dorsal lobe and passing to the vertex. Arising near the origin of the latter nerves are the roots of the *œsophageal ganglia.* According to some authorities the fibres of the paired nerves supplying the median ocellus take their origin from the deutocerebrum.

The TRITOCEREBRUM is formed by the ganglia of the third or intercalary segment of the head. It is divided into two small widely separated lobes which are attached to the dorsal lobe of the deutocerebrum and receive nerve fibres from the latter. The tritocerebral lobes are joined together by means of the *post-œsophageal commissure* which passes immediately behind the œsophagus. They also give origin to (1) the *para-œsophageal connectives* or *crura cerebri* which unite the brain with the subœsophageal ganglion, and (2) the *labro-frontal nerves.* Each of the latter consists of two bundles of fibres, one of which passes to the labrum as the *labral nerve,* and the other forms the root of the frontal ganglion.

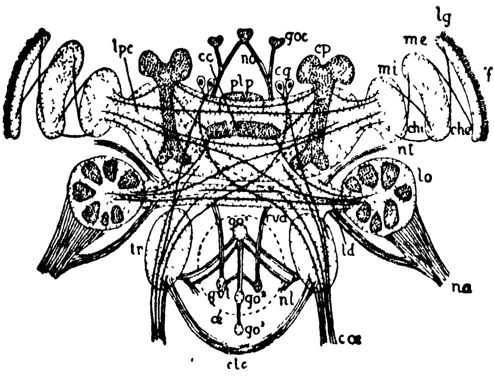

FIG. 61.—DIAGRAM OF THE BRAIN AND VISCERAL NERVOUS SYSTEM OF A CRICKET (much of the cortical layer has been omitted).

cc, central body; *cg,* ganglion cells; *che,* external chiasma; *chi,* internal chiasma; *cœ,* para-œsophageal connective; *cp,* mushroom body; *ctc,* post-œsophageal (tritocerebral commissure); *fpr,* post-retinal fibres; *goc,* ocellar ganglion; go_1, hypocerebral ganglion; go_2, go_3, unpaired visceral ganglia; *gvl,* œsophageal ganglion; *ld,* dorsal lobe of deutocerebrum; *lg,* periopticon; *lo,* olfactory (deutocerebral) lobe; *lpc,* protocerebral lobe; *me,* epiopticon; *mi,* opticon; *na,* antennary nerve; *nl,* labral nerve; *no,* ocellar nerve; *nt,* tegumentary nerve; *œ,* outline of œsophagus; *plp,* posterior dorsal commissure; *rvd,* root of œsophageal ganglion; *tr,* tritocerebrum. *After* Viallanes, *Ann. Sci. Nat.* 1893.

2. The **Subœsophageal Ganglion** is the ventral ganglionic centre of the head and is formed by the fusion of the ganglia of the mandibular, maxillary and labial segments. It gives off paired nerves supplying their respective appendages.

3. The **Ventral Nerve Cord** consists of a series of ganglia lying on the floor of the thorax and abdomen. They are united into a longitudinal chain by means of a pair of connectives which issue from the posterior border of the subœsophageal ganglion. The first three ganglia are situated one in each of the thoracic segments, and are known as the thoracic ganglia; the remainder lie in the abdomen and form the ganglia of that region.

The *thoracic ganglia* control the locomotory organs. Each ganglion gives off two pairs of principal nerves, one of which supplies the general musculature of the segment and the other innervates the muscles of the legs. In the meso- and meta-thorax an additional pair of nerves is present which controls the movements of the wings.

The *abdominal ganglia* are variable in number; in *Machilis* and in many larvæ there are eight ganglia in the abdomen but as a rule there are fewer. The first abdominal ganglion frequently coalesces with that of the metathorax and the terminal ganglion is always composite. The latter is of the nature of a ganglionic centre formed by the fusion of at least three primitive ganglia. Each abdominal ganglion gives off a pair of principal nerves to the muscles of its segment.

(*b*) The Visceral Nervous System

The visceral or sympathetic nervous system is divided into œsophageal sympathetic and ventral sympathetic systems.

1. The ŒSOPHAGEAL SYMPATHETIC (or STOMATOGASTRIC) NERVOUS SYSTEM (Fig. 62) is directly connected with the brain and innervates the fore and middle intestine, heart and certain other parts. It is dorsal in position, lying above and at the side of the fore-intestine and is divisible into two principal types as below.

The first type is well exhibited in the Blattidæ and is composed of the following ganglia and nerves. A small triangular *frontal ganglion* lies above the œsophagus, a short distance in front of the brain. Anteriorly it gives off a *frontal nerve* which passes to the clypeus, and a pair of lateral roots connect the frontal ganglion with the tritocerebrum. Posteriorly the frontal ganglion gives off a *recurrent nerve* which extends along the mid-dorsal line of the œsophagus and, passing just beneath the brain, expands a short distance behind the latter centre into a *hypocerebral ganglion*.[1] The recurrent nerve leaves the hypocerebral ganglion and passes backwards to the hinder region of the fore-intestine, where it terminates in a *ventricular* or *stomachic ganglion*. The latter innervates the adjacent region of the fore and middle intestine. A pair of *œsophageal* or *pharyngeal ganglia* lies on the œsophagus just behind the brain and each ganglion is joined with the hypocerebral ganglion. They are also connected with the deutocerebrum by roots which have already been alluded to. Closely associated with the œsophageal ganglia are the corpora allata (vide p. 137) which were formerly referred to as posterior œsophageal ganglia.

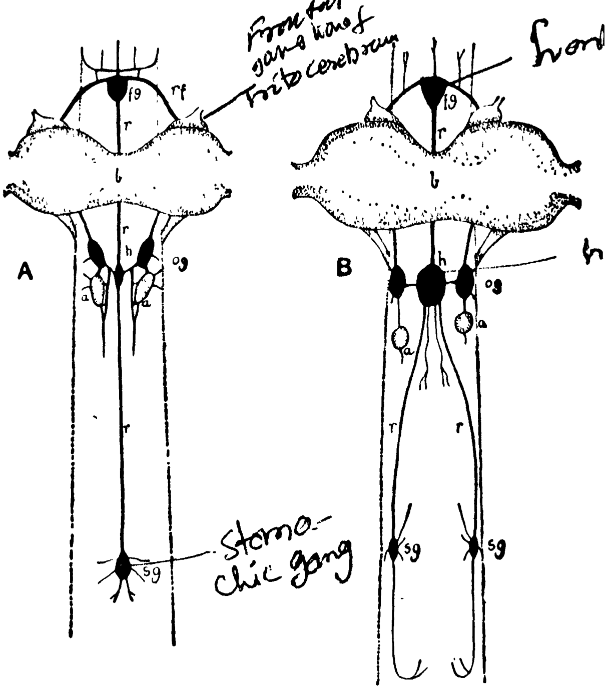

FIG. 62.—SEMI-DIAGRAMMATIC FIGURES OF TWO PREVALENT TYPES OF SYMPATHETIC NERVOUS SYSTEM (IN BLACK).

A, with a single recurrent nerve and stomachic ganglion ; B, with paired recurrent nerves and ganglia. The fore-intestine is represented by the dotted lines. *a*, *a*, corpora allata ; *b*, brain ; *fg*, frontal ganglion ; *h*, hypocerebral ganglion ; *og*, œsophageal ganglion (right) ; *r*, recurrent nerve ; *rf*, root of frontal ganglion ; *sg*, stomachic ganglion.

The second type of œsophageal nervous system (exhibited for example in the saltatorial Orthoptera) differs in that the stomatogastric nerve is paired, each nerve terminating in a separate ventricular ganglion.

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[1] In the Blattidæ and certain other families the hypocerebral ganglion is more or less atrophied.

The VENTRAL SYMPATHETIC NERVOUS SYSTEM (Fig. 63) when typically veloped, consists of a pair of transverse nerves associated with each ganglion of the ventral nerve cord, and each pair is connected with the ganglion preceding it by a median longitudinal nerve. The transverse nerves pass to the spiracles of their segment and dilate into one or more small ganglionic enlargements along their course. Arising from the last abdominal ganglion are the *splanchnic nerves* which pass to the hind-intestine and the reproductive system.

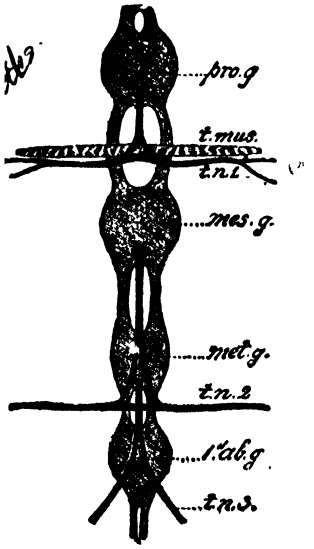

FIG. 63.—THORACIC GANGLIA AND PORTION OF SYMPATHETIC NERVOUS SYSTEM OF A *CHIRONOMUS* LARVA.

pro g, mes g, met g, thoracic ganglia; *1ab g*, 1st abdominal ganglion; *t.mus*, transverse muscle; tn_1–tn_3, sympathetic nerves. *After* Miall and Hammond.

The Peripheral Sensory Nervous System (Fig. 64)

This system is composed of an exceedingly delicate plexus of nerve fibres and multipolar nerve cells situated in the integument below the hypodermis. Certain of the processes of the nerve cells are continuous with those of bipolar nerve cells whose terminal prolongations innervate the sensory hairs on the general surface of the body. The larger fibres of this plexus are derived from the paired nerves of the central nervous system (vide Zwarzin, 1912).

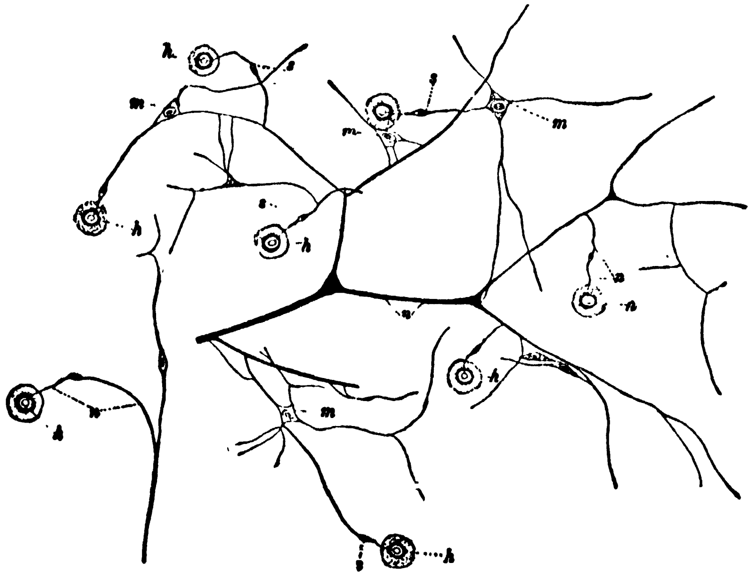

FIG. 64.—PORTION OF THE PERIPHERAL SENSORY NERVOUS SYSTEM OF A SILKWORM.

h, h, bases of sensory hairs; *s, s*, bipolar nerve cells; *m, m*, multipolar nerve cells; *n, n*, nerves. *After* Hilton, *Amer. Nat.* 36.

II. Modifications of the Nervous System (Fig. 65)

There are many grades of cerebral development in insects and Viallanes considered that the brain of a locust differs as greatly in structure from that of a wasp as the brain of a frog does from that of man. The optic lobes, for example, are very large in species with highly developed compound eyes and poorly developed, or absent, in those with degenerate visual organs or without eyes. The antennal lobes show similar relations between the development of those areas and of the senses correlated with them. As regards the internal structure of the brain, there is a wide range in the degree of development of the mushroom bodies. Many investigators have observed the large number of sensory and motor nerve tracts that are concentrated in these areas, and it is probable that, in the mushroom bodies, the main sensory impressions are received, actions coördinated and associations once acquired are impressed. The greatest development of these bodies is found among Hymenoptera, where they attain a size and complexity not found elsewhere. This specialization corresponds in a general way with the highly evolved phases of behaviour displayed among members of that order. Jonescu (1909) has shown that structural differences in the brain in drone, worker and queen bees appear to be correlated with the degree of development of the special instincts and activities of the three forms. Von Alten (1910) and Armbruster (1919) have compared the ratio of the size of the mushroom bodies to the brain as a whole obtaining, in this way, a kind of brain index. On the basis of such numerically expressed relationships the sawflies come lowest on the scale, the social Hymenoptera highest, while the solitary bees occupy an intermediate position. It is not possible, however to draw general deductions of this kind since comparative studies have yet to be made in other orders.

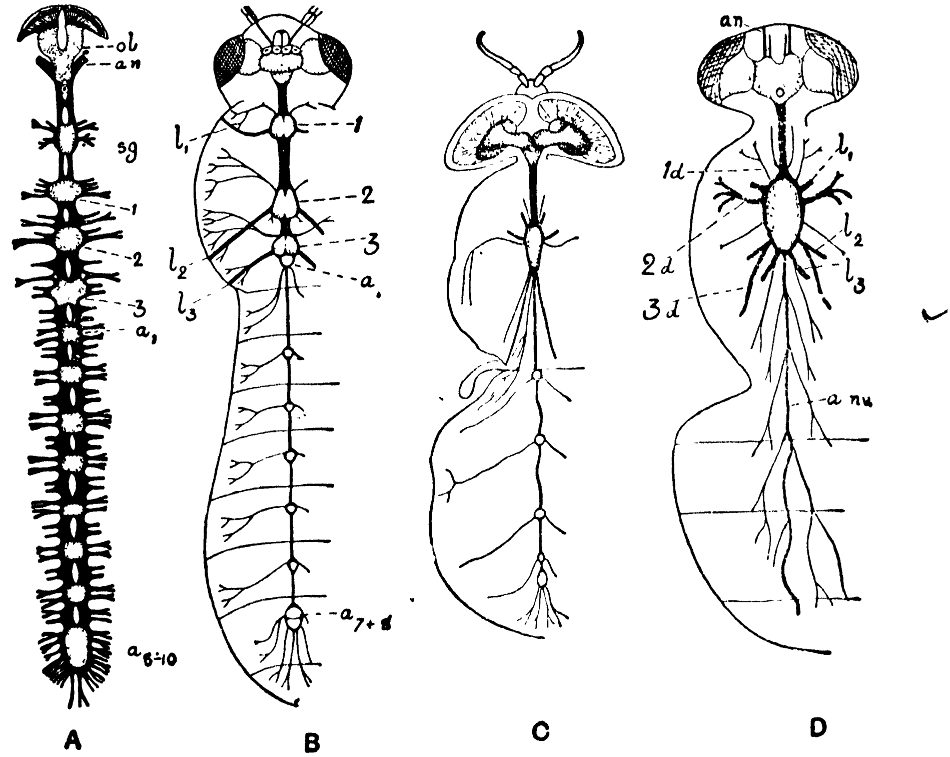

FIG. 65.—SCHEMATIC FIGURES OF THE CENTRAL NERVOUS SYSTEM SHOWING DEGREES OF CONCENTRATION, BASED UPON VARIOUS AUTHORS.

A, *Machilis* (Oudemans); B, *Chironomus* (Brandt); C, *Stratiomyia* (Kunckel d'Herculais); D, *Musca* (Hewitt). 1–3, thoracic ganglia; a_1, a_7–$_8$, a_8–$_{10}$, abdominal ganglia; *an*, antennary nerve; *ol*, optic lobe; *sg*, sub-œsophageal ganglion; l_1–l_3, nerves to legs; 1*d*–3*d*, dorsal thoracic nerves; *a.nv*, abdominal nerve cord.

According to Dujardin the volume of the brain is equivalent to $\frac{1}{174}$th the volume of the body in *Apis*, $\frac{1}{280}$th in *Formica*, $\frac{1}{3290}$th in *Melolontha* and $\frac{1}{4200}$th in *Dytiscus*.

The most generalized condition of the ventral nerve cord is found in the Thysanura, the lower Pterygota and in many larvæ: in these instances three thoracic and eight abdominal ganglia are present. In *Melanoplus*, *Periplaneta* and other of the lower Pterygota, however, there is a reduction in the number of abdominal ganglia; in *Tabanus* the thoracic ganglia are fused into a single centre and the six abdominal ganglia are very much concentrated. In *Volucella zonaria* the thoracic ganglia are similarly fused into a common centre and the abdominal ganglia have coalesced into two centres. In the Sminthuridæ among Collembola, in certain families of Coleoptera, and in the great majority of the higher Diptera, the whole of the thoracic and abdominal ganglia are concentrated in a single mass which, in the last two instances, is located in the thorax. Among the Coccidæ centralization has proceeded still further, the subœsophageal ganglion being incorporated in the common thoracico-abdominal centre. Specialization along these lines is by no means confined to the most highly evolved insects and appears, in many cases, to be correlated with a reduction in the length and segmentation of the abdomen which results in a forward migration of the ganglia.

III. Physiology of the Nervous System

The experimental results derived from the study of the nervous system may be summarized briefly as follows:

The brain is the chief seat of sensation and is also the most important coördinating centre of the body. On the other hand, its capacity as a motor centre is very limited and is mainly concerned with the antennal movements. Removal of the brain renders an insect inert and it is no longer able to exert initiatory impulses that lead to the performance of instinctive acts. Brainless insects can, however, be artificially stimulated to walk or fly, and they will feed if the food be placed in contact with the mouth-parts, but there is no power of detecting food if the latter be placed even a short distance away. The subœsophageal ganglion controls the movements of the mouth-parts and the loss, or destruction, of this centre results in inability to feed. Decapitated insects appear to lose both their initiatory and inhibiting centres, but can be artificially stimulated to oviposit and are able, to some extent, to walk and fly. Several observers have shown that the cephalic ganglia exercise an inhibitory influence upon reflex responses and experiments by Kopéc, on the gypsy moth, suggest that the actual centre involved is not the brain but the subœsophageal ganglion. After destruction of the latter centre strong reflexes result from artificial stimulation which produces less pronounced responses in the uninjured insect. Decapitation has little effect upon respiratory movements, beyond a temporary disturbance, and their controlling centres are located elsewhere. The œsophageal sympathetic system comprises both sensory and motor nerve fibres and the recurrent nerve, through the medium of the frontal ganglion, controls the movements of the fore-intestine. According to Faivre, destruction of the frontal ganglion, or section of the roots which connect it with the brain, results in cessation of the power of swallowing. The sensory and motor centres concerned with locomotion are located in the thoracic ganglia. Each thoracic ganglion exhibits considerable autonomy and the severance of the connectives behind and in front of the prothoracic ganglion does not prevent the fore-legs from responding to stimulation. Similarly, after section of the connectives between the meso- and meta-thoracic ganglia the regions before and behind the lesion retain their powers of movement and sensation. The lateral nerves of the thoracic and abdominal segments divide within their respective ganglia into two roots as was shown in 1894 by Binet (Fig. 66). The fibres of the dorsal roots terminate in motor cytons, while those of the ventral roots are sensory and end in complex arborizations (Zwarzin, 1924). Binet concluded that the fibres were thus distributed from studies in Coleoptera with immobile elytra, where the ventral or sensory roots alone are present in the mesothoracic ganglion ; Zwarzin has confirmed and extended the work of Binet by using modern neurological technique. The functions of the abdominal nerve cord are obviously best investigated among insects whose ganglia have undergone least fusion. A number of investigators, of whom the most recent is Stahn (1928), have shown that each abdominal ganglion functions as a local centre controlling respiratory movements. It is, however, further evident that a second respiratory centre is located in the prothoracic ganglion. This centre appears to be influenced by the oxygen and carbon dioxide content of the medium, whereas the abdominal centres are apparently primarily concerned with the actual ventilation of the tracheal system. In the abdomen is located the centre for the reflexes governing oviposition and, according to Kellogg, the living abdomen of the female silkworm moth, when separated from the thorax, can be fertilized by the male and stimulated to lay fertile ova. According to Faivre, control of the reproductive organs, and of the muscles of the hind-intestine, is localized in the last abdominal ganglion which he terms the genito-splanchnic centre.

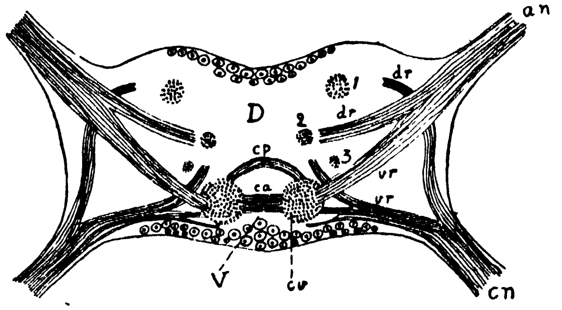

FIG. 66.—SCHEMATIC TRANSVERSE SECTION THROUGH A THORACIC GANGLION OF AN INSECT ACCORDING TO BINET.

D, dorsal lobe ; V, ventral lobe ; 1, 2, 3, groups of dorsal connecting fibres ; *an*, alary nerve ; *ca*, anterior ventral commissure ; *cp*, posterior do. ; *cv*, ventral column ; *cn*, crural nerve ; *dr*, *vr*, dorsal and ventral roots ; *e*, epineurium.

Among insects, therefore, there is relatively little centralization of function in the nervous system. In the absence of the brain complex reflexes can be induced provided the specific ganglionic centre, and the nerves concerned, are intact.

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THE SENSE ORGANS

THE faculty of appreciating differences between the external forces acting upon it enables an animal to maintain its existence. Nerve fibres alone are not adapted to receive the impressions of these forces to an adequate degree. Special mechanisms are consequently necessary in order to differentiate between the various and often minute forces acting on the organism. Such mechanisms are of various kinds and differ according to the nature of the stimuli which they are capable of appreciating. These structures are the sense organs or receptor organs.

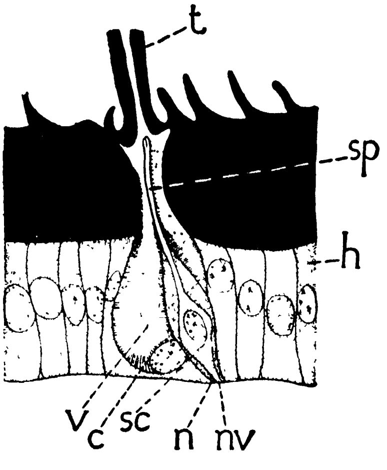

FIG. 67.—SIMPLE TRICHOID SENSILLA FROM THE CERCUS OF *GRYLLUS CAMPESTRIS* (cuticular parts deep black).

c, trichogenous cell; *h*, hypodermis; *n*, neurilemma; *nv*, nerve fibre; *sc*, sense cell and its process *sp*; *t*, base of hair; *v*, vacuole. From Sihler.

The simplest types of sense organs are termed *sensillæ.* In their least modified form they closely resemble ordinary body hairs but differ in having acquired connection with the nervous system and are thereby enabled to appreciate external stimuli. The elements which form a typical sensilla are the cuticular or external part of the organ and its special trichogenous or formative cell, and a sense cell. The sense cell lies in the hypodermis and its distal process penetrates the trichogenous cell to enter the cavity of the cuticular part of the sensilla. Very often, at the end of the sensory process, there is a minute sense rod or *scolopale* which attaches it to a point on the cuticle of the organ (Figs. 67 and 101). The sensory cell is to be regarded as a special hypodermal cell which is connected with a nerve fibre. When the nerve fibre is traced inwards to its ganglion of the central nervous system it ends in fine ramifications. As in other invertebrates the only sensory cells detected in insects are those lying in the hypodermis. This is in sharp contrast to vertebrates whose sensory cells have come to lie internally, close to the central nervous system: those concerned with the olfactory nerve alone retain the primitive condition (Bayliss). Fig. 68 is a diagram of the insect nervous system. A given stimulus impresses itself upon the sensilla (or sensillæ) concerned and an impulse is conveyed by afferent nerve fibres to an association centre in the central nervous system. The association centre is linked with a motor centre from which efferent nerve fibres pass to the muscles. The association centre is a kind of two-way connection between the roots of the sensory and motor nerves. The degree of development of such centres varies greatly and, in the mushroom bodies of the brain for instance, there are large

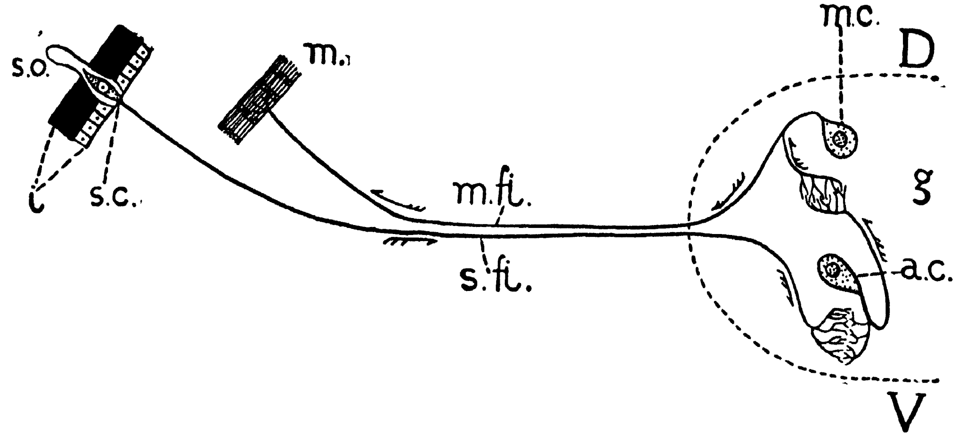

Fig. 68.—Diagram of the Reflex Mechanism of the Nervous System of an Insect. One half of a ganglion, *g*, of the ventral nerve cord is represented in outline.

D, dorsal aspect; *V*, ventral aspect. A motor (*m.fi.*) and a sensory fibre (*s.fi.*) of a lateral nerve are shown; *i*, integument; *s o*, sense organ; *s c*, sensory cyton or cell; *m*, muscle; *a c*, association cyton; *m.c*, motor cyton. (The course traversed by a stimulus, received by the sense organ, is represented by arrows)

numbers whose nerve fibres link different parts of the nervous system together.

The sense organs of touch, taste, and smell remain for the most part as isolated sensillæ. Those of sight and hearing are usually composed of aggregations of sensillæ, forming more elaborate organs which are essentially localized in position.

Since the cuticular parts of the sensillæ, other than those of sight and hearing, are to be regarded as modified setæ, these organs are often alluded to as the skin, or setiferous, sense organs. Many types of the latter have been described among insects, and they have received various names based upon characters afforded by their cuticular parts. The following classification (Figs. 69–72) includes the common kinds and is largely based on those of Schenk (1903) and Berlese. It must be remembered, however, that these types are often not sharply differentiated and various intermediates exist between them.

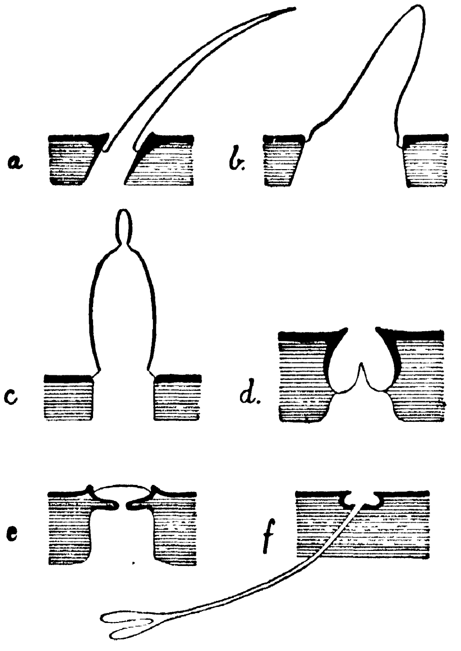

Fig. 69.—Cuticular Portions of Setiferous Sense Organs.

a, trichoid (palp of *Calliphora*); *b*, basiconic (*Acrida*; *c*, styloconic (haustellum of a Lepidopteron), *d*, cœloconic (*Acrida*); *e*, placoid (*Ophion*); *f*, ampullaceous (anti). Semidiagrammatic, based upon various authors.

(*a*) *Trichoid.*—Setiform, and articulated with a base which is set below the general surface of the cuticle.

(*b*) *Basiconic.*—Conical and immobile, arising from the general surface of the cuticle.

(*c*) *Styloconic.*—(Biarticulate type of Berlese.) Differs from the basiconic sensilla in consisting of one or more pegs of the basiconic type which are elevated on a style or cone.

(*d*) *Placoid.*—Consisting of a plate or membrane covering an enlarged pore canal (*e*) *Cœloconic*.—Derived from a basiconic sensilla by the latter becoming sunk into a pit with its apex not projecting.

(*f*) *Ampullaceous* (Flask-shaped organs of Lubbock and Forel).—Derived from a cœloconic sensilla by the pit becoming prolonged deeply inwards to form a narrow canal. The latter becomes swollen, at its extremity, into an ampulla which encloses a slender hair-like process.

The different kinds of sense organs are distinguished according to the nature of the stimuli that they are adapted to receive. The tactile organs respond to simple contact with external objects and the auditory organs to vibratory motion induced by sound waves. These two kinds of organs may therefore be classed as the mechanical sense organs. The organs of smell and taste respond to chemical stimuli, acting either at a distance or by direct contact, and may be referred to as the chemical sense organs. The organs of light respond to the stimulus of light and are probably adapted to make use of a photochemically sensitive substance, but, to be of value as distance receptors, it is necessary for them to be able to form images of external objects.

It is noteworthy that static organs enabling the insect to orient itself in a required plane, and so preserve its balance, when in locomotion, have not been detected in the class as a whole. The possibility, however, that the chordotonal organs (p. 89), which have been found in almost all orders, may perform this function is an unexplored problem.

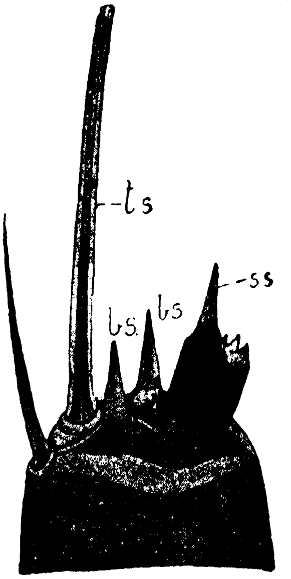

FIG. 70.—APEX OF THE ANTENNA OF THE LARVA OF *MAMMESTRA PISI*.

bs, basiconic sensillæ; *ss*, styloconic sensilla; *ts*, trichoid sensilla. *After* Nagel, *Bibl. Zoolog.* 1894.

1. The Tactile Sensillæ

The tactile sensillæ of insects are often distributed over the entire integument, a feature which is well exhibited for example in lepidopterous larvæ. For the most part these organs attain their greatest abundance on the antennæ, palpi, legs, and cerci. The sensitiveness of insects to tactile impressions is due to the number and wide distribution of these organs over the body, rather than to any elaboration of their structure.

Tactile sensillæ include the simplest of all the special sense organs and are of the trichoid type. Apart from the presence of nerve fibres in association with them, there is often little to distinguish them from ordinary clothing hairs. They may be either slender flexible structures, or stouter and bristle-like, both types often occurring together on the same appendage. Each is located over a pore-canal in the integument and is associated with an underlying bipolar nerve-cell. The latter is prolonged at one extremity into a nerve fibre, which enters the cavity of the hair and, in some cases, the fibre may be branched. In lepidopterous larvæ, Hilton has shown that the nerve-cells are connected with the peripheral nervous system.

2. The Olfactory and Gustatory Sensillæ

The senses of taste and smell are higher developments of a primitive chemical sense; the chief difference between the two kinds of sensation

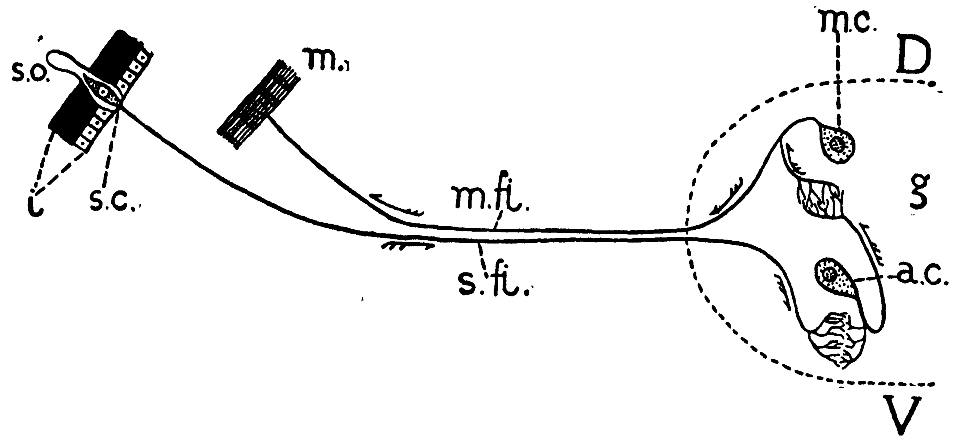

FIG. 68.—DIAGRAM OF THE REFLEX MECHANISM OF THE NERVOUS SYSTEM OF AN INSECT. One half of a ganglion, *g*, of the ventral nerve cord is represented in outline.

D, dorsal aspect; *V*, ventral aspect. A motor (*m.fi.*) and a sensory fibre (*s.fi.*) of a lateral nerve are shown; *i*, integument; *s.o*, sense organ; *s.c*, sensory cyton or cell; *m*, muscle; *a.c*, association cyton; *m.c*, motor cyton. (The course traversed by a stimulus, received by the sense organ, is represented by arrows.)

numbers whose nerve fibres link different parts of the nervous system together.

The sense organs of touch, taste, and smell remain for the most part as isolated sensillæ. Those of sight and hearing are usually composed of aggregations of sensillæ, forming more elaborate organs which are essentially localized in position.

Since the cuticular parts of the sensillæ, other than those of sight and hearing, are to be regarded as modified setæ, these organs are often alluded to as the skin, or setiferous, sense organs. Many types of the latter have been described among insects, and they have received various names based upon characters afforded by their cuticular parts. The following classification (Figs. 69–72) includes the common kinds and is largely based on those of Schenk (1903) and Berlese. It must be remembered, however, that these types are often not sharply differentiated and various intermediates exist between them.

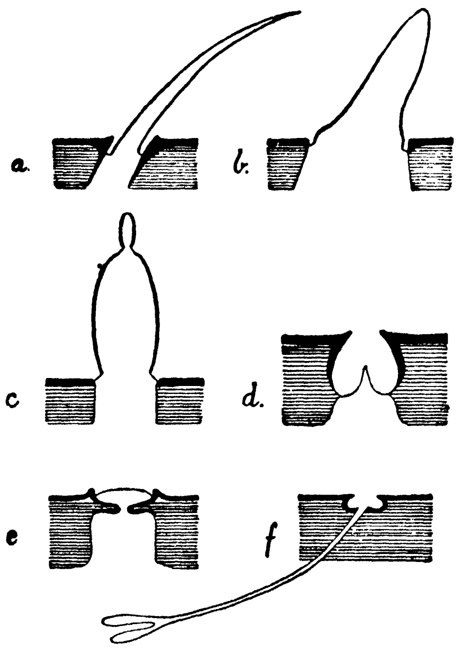

FIG. 69.—CUTICULAR PORTIONS OF SETIFEROUS SENSE ORGANS.

a, trichoid (palp of *Calliphora*); *b*, basiconic (*Acrida*; *c*, styloconic (haustellum of a Lepidopteron); *d*, cœloconic (*Acrida*); *e*, placoid (*Ophion*); *f*, ampullaceous (anti). Semidiagrammatic, based upon various authors.

(*a*) *Trichoid.*—Setiform, and articulated with a base which is set below the general surface of the cuticle.

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(*d*) *Placoid.*—Consisting of a plate or membrane covering an enlarged pore canal

is that smell is the perception of chemical stimuli, acting from a distance, whereas taste has scarcely any distance element, even in its most developed form (Bayliss). It is, therefore, not surprising that the sense of smell is much more delicate than that of taste, and its receptor organs are often more highly developed.

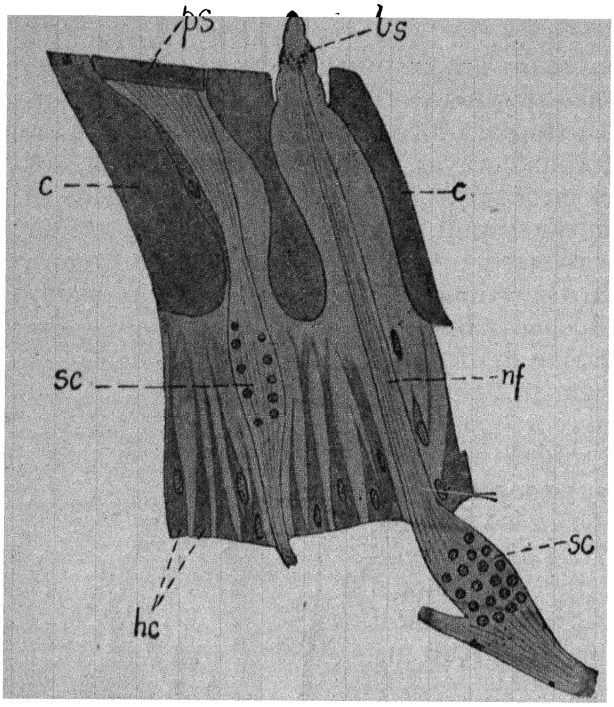

Fig. 71.—Basiconic (*bs*) and Placoid Sensillæ (*ps*) from a Worker of *Vespa crabo*.

c, cuticle; *hc*, hypodermal cells; *nf*, nerve fibre; *sc*, sensory cells. *After* Nagel.

Since there appears to be no constant structural difference between olfactory and gustatory sensillæ in insects it is desirable to discuss them together. It is also probable that in many cases the two kinds of sensation are not sharply demarcated.

A large number of experiments have been conducted with a view to locating the olfactory sense in insects, and the majority of observers agree in regarding it as being mainly concentrated in the antennæ. Histologists have examined the sensillæ present on those appendages, and have ascribed an olfactory function to various types. The problem, however, is by no means a straightforward one, as similar kinds of sensillæ may occur over the body, and on the palpi and cerci. Also, the antennæ of many insects bear several very different types of sensillæ. It has been found experimentally that, in some insects, the olfactory sense is definitely restricted to the antennæ. Thus Barrows (1913) ascertained that *Drosophila* no longer responds to odorous substances when the terminal joint of the antennæ is amputated. Certain other insects still react to volatile substances after the antennæ have either been amputated, or coated with paraffin wax, although the response takes place more tardily, thus implying a wider distribution of the olfactory organs.

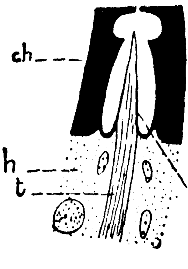

Fig. 72. Cœloconic Sensilla (*k*) of *Apis mellifica*.

ch, cuticle; *h*, hypodermis; *t*, nerve. *After* Schenck, *Zool. Jahrb. Morph.* 1903.

There appears to be little doubt that the various types of sensillæ on the mouth-parts and epipharynx are chemoreceptors of taste. While this conclusion is mainly based on morphological evidence, the physiological studies of Kunze (1927) and of von Frisch (1927–30) afford support to the contention as regards gustatory perception in the honey bee. There is, furthermore, considerable experimental evidence fromthe work of Minnich (1922, 1926, 1929) and of Crow (1932) that gustatory perception, in some insects, also takes place by means of the tarsi. Minnich observed that certain Nymphalid butterflies uncoiled the proboscis when in proximity to food materials and that the receptors concerned are located in the tarsi.

Analogous responses were obtained by Minnich and by Crow with Muscid flies in the presence of appropriate sugar solutions. Under certain conditions these insects were able to distinguish saccharose solutions as dilute as M/25, 600 from water.

The principal types of sensillæ which have been regarded as chemical receptors include the various kinds of thin-walled structures enumerated under *b-f* on p. 72. They occur over the general surface of the parts bearing them (Figs. 71 and 72) or they may be localized in sac-like invaginations of the integument, forming organs of a higher type (Figs. 73 and 74). The latter are well exhibited, for example, in the flask-like pocket found on the apical palpal joint in various Lepidoptera (vide vom Rath, 1896) and in the antennal pits of many of the higher Diptera (vide Smith, 1919). The number of sensillæ present in an insect is often exceedingly great. Thus in *Melolontha* Hauser (1880) states that there are 39,000 cœloconic sensillæ to each antenna in the male, and 35,000 in the female. In the hive bee Vogel (*Zool. Anz.* 1922) finds that there are about 2,000 placoid sensillæ to each antenna in the queen, about 6,000 in the worker and about 30,000 in the male.

Chemotropism or the response of an organism to olfactory stimuli is a phenomenon of very great significance in the biology of insects. It is particularly in evidence in the selection by many insects of their food, by the female when she chooses particular plants for oviposition, and by the male when in pursuit of the female.

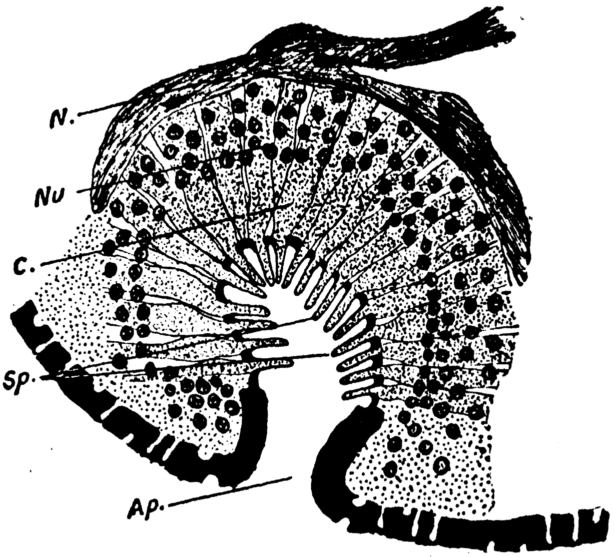

FIG. 73.—SECTION THROUGH AN ANTENNAL SENSORY PIT OF A SYRPHID (*SERICOMYIA BOREALIS*).

C, sensory cells and their nuclei *Nu*; *Ap*, aperture of sensory pit; *Sp*, sensillæ; *N*, nerve. *After* K. M. Smith, *Proc. Zool. Soc.* 1919.

Little is known of the physiology of olfactory perception in insects. Vapours before acting upon the nerve ending of a sensilla must, in some way, enter into solution in a liquid either outside or inside the organ. One hypothesis claims that the cuticular parts of the olfactory sensillæ are kept moist by a film of secretion which reaches the exterior through the covering membrane or by means of minute pores in the latter. The existence of such a film, however, is difficult to detect and has yet to be affirmed. The alternative hypothesis holds that the covering membrane itself is of a texture directly permeable to vapours which enter into solution upon coming in contact with the vacuolar liquid surrounding the nerve endings (Figs. 67 and 101).

Verschaffelt (1910) has shown that the larval food-plants of *Pieris rapæ* and *P. brassicæ* contain a group of glucosides—the mustard oils. He took a solution of sinigrin, which is present in black mustard, and uniformly distributed it over the leaves of plants which the *Pieris* larvæ had previously refused to eat. Leaves so treated were readily devoured, and from such experiments it appears that these larvæ exhibit strong chemotropism towards mustard oils whose presence in the leaves of certain plants determines the selection of the latter by the larvæ for their food. By a similar method of research Verschaffelt has shown that larvæ of the sawfly, *Priophorus* (*Cladius*) *padi*, which feed on certain of the Rosaceæ, are attracted by the glucoside amygdalin. Howlett (1914) has noted a marked response of certain Thysanoptera to the stimulus of the odours of benzaldehyde, cinnamylaldehyde and anisaldehyde. Chatterjee in India has discovered that Kusum oil has a marked attraction for both sexes of the Coreid *Serinetha augur*. Dewitz ascertained that it is the odour of the nectaries of the vine flowers that attracts the vine moths and induces them to oviposit on the unopened buds. Barrows (1907) has proved that *Drosophila ampelophila*, which lays its eggs in fermenting fruit, exhibits an optimum response to a mixture of ethyl alcohol of 20 per cent. strength and acetic acid of 5 per cent. It is noteworthy that cider vinegar, and fermented cider, contain alcohol and acetic acid in percentages very close to those just quoted. Crumb and Lyon (1917) have produced evidence suggesting that carbon dioxide is the chief stimulus inducing oviposition in the house fly, and Richardson (1916) finds that ammonia exercises a marked attraction for those Diptera which spend part of their lives in some form of animal excrement. Imms and Husain (1920) have conducted experiments showing that many Diptera are more strongly attracted to esters rather than to the respective acids or alcohols.

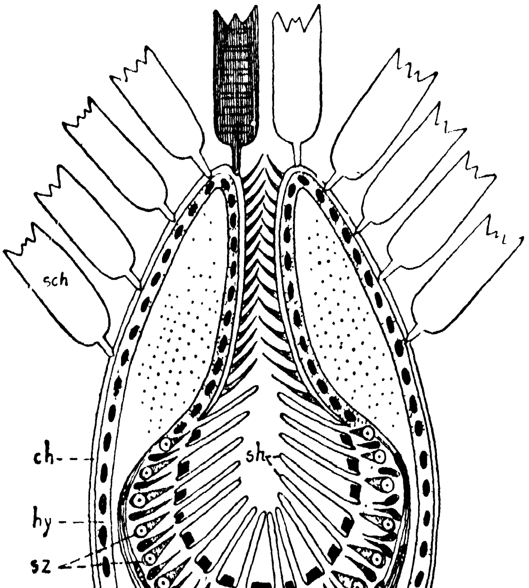

Fig. 74.—Longitudinal Section through the Apex of the Labial Palp of *Pieris brassicæ*, showing Sensory Pit.

ch, cuticle ; *hy*, hypodermis ; *n*, nerve ; *sch*, scales ; *sh*, sensillæ ; *sz*, sensory cells. *After* vom Rath, *Zeits. wiss. Zool.* 1888.

The remarkable phenomenon known as "assembling," which is particularly prevalent among moths belonging to the Lasiocampina, is another example of chemotropism. The females emit an odour to attract the opposite sex and, under favourable conditions, a freshly emerged example of the sex will attract scores of males which fly up against the breeze. Schenk (1903) has compared the number of antennal sensillæ of certain types in the two sexes of species in which the antennæ exhibit pronounced sexual dimorphism in correlation with differences of sexual behaviour. In certain species the ratios of their numbers in the male and female were from 3·5 : 1 to 8 : 1. Howlett (1915) has discovered a chemotropic phenomenon in certain species of *Dacus*, the males of *D. diversus* being strongly attracted by isoeugenol, *D. zonatus* by methyl-eugenol, and *D. ferrugineus* by both reagents. The significance of these responses is not properly understood, but it is noteworthy that females are not attracted by the substances mentioned.

Forel and others have shown that ants are guided in their foraging expeditions by means of their contact-odour sense: they recognize by means of their antennal sense organs the odour-form, and hence also the direction of the trails laid down by their own feet and those of their nestmates. Blind or small-eyed ants follow these odoriferous trails very closely, relying upon their topochemical sense in finding their way back to the nest (Wheeler). Ants also react amicably towards the odour of members of their own colony, and by this means they are able to distinguish between "friends" and "aliens."

3. The Organs of Sight

Two types of eyes are found in insects, viz. : *ocelli or simple eyes*, and *compound* or *faceted eyes.* Typically both kinds occur in the same insect but, on the other hand, either or both may be absent. Ocelli are often lacking in the imagines and compound eyes are wanting in larvæ. Visual organs of any kind are usually absent in larvæ which live in situations concealed from the light. Among adult insects they are either wanting, or exhibit various stages of degeneration, in cavernicolous forms and in various species which inhabit the nests of termites and ants. They are also wanting or degenerate in many of the Anoplura, in the sterile castes of almost all termites, and in the workers of certain ants. The two types of eyes are treated separately below.

A. THE OCELLI

Ocelli are divided into two classes : (1) the *dorsal or primary ocelli* of adult insects, and nymphs : and (2) the *lateral ocelli* which are the usual larval eyes.

1. THE DORSAL OCELLI. The dorsal ocelli are innervated from the ocellar lobes which are located in the protocerebrum, between the mushroom bodies. When typically developed they are three in number disposed in a triangle. In the Plecoptera they are borne on the frons, and in certain other insects the median ocellus is situated on the frons, while the paired ocelli are located in the suture between that region and the vertex. In the more specialized orders the ocelli are usually situated on the vertex.

The median ocellus exhibits evidence of a paired origin since the root of the nerve supplying it is double, whereas the nerve-roots of the other ocelli are single. In some insects (e.g. Odonata, *Bombus*) the median ocellus exhibits a bilateral structure which is never found in the remaining ocelli.

The dorsal ocelli greatly vary in the details of their structure in various insects, but they exhibit certain common essential features and the following parts can be distinguished (Fig. 75).

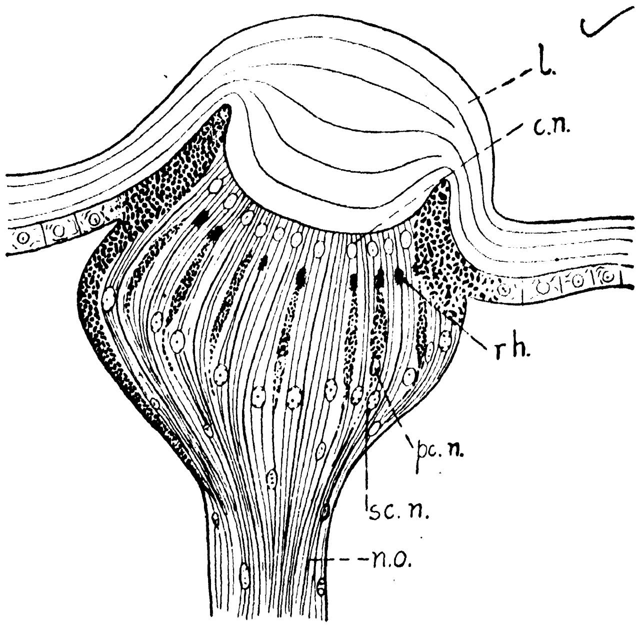

FIG. 75.—SECTION THROUGH AN OCELLUS OF *APHROPHORA SPUMARIA.*

cn, nucleus of corneagen cell; *l*, lens; *no*, ocellar nerve; *pc.n*, nucleus of pigment cell; *rh*, rhabdom; *sc.n*, nucleus of retinulæ. *After* Link, *Zool. Jahrb. Morph.* 1908.

(*a*) *The cornea.*—The name cornea is given to that portion of the cuticle which is arched or raised to form the external investment of the ocellus. In this region the cuticle is more transparent than elsewhere and usually becomes thickened to form a more or less spherical body known as the *lens*. In rare instances (Ephemeroptera, Fig. 76) the cornea is arched but not thickened and the lens is formed by a mass of polygonal cells lying beneath the corneagen layer (vide Hesse 1901, Seiler 1905).

(*b*) *The corneagen layer.*—This layer is directly continuous with the hypodermis but differs in being composed of colourless transparent cells which secrete and afford support to the lens. In some insects its cells become elongated and grouped together to form the *vitreous body* which supplements the lens in its function.

(*c*) *The retina.*—The retina is composed of *visual cells* which are nerve end-cells, each being in direct connection with the termination of a fibre of the ocellar nerve. The visual cells are associated together in groups of two, three or more cells, each group being termed a *retinula*, which surrounds a longitudinal optic rod or *rhabdom*. The latter is produced along the inner junctions of the component cells of a retinula, and varies in form according to the number of those cells present.

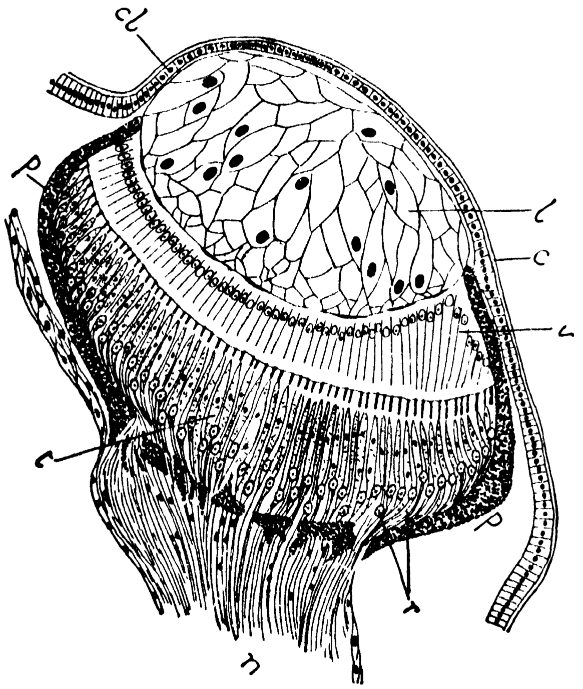

FIG. 76.—SECTION OF THE MEDIAN OCELLUS OF *CHLŒON*.

c, cuticle; *cl*, corneagen layer; *l*, cellular lens; *v*, vitreous layer; *r*, retinulæ; *t*, tapetum; *p*, pigment; *n*, ocellar nerve. *After* Hesse, 1901.

(*d*) *Pigment cells.*—In some ocelli there are accessory cells loaded with pigment situated between the retinulæ, or the pigment may be contained within the visual cells themselves. In deeply pigmented ocelli the margin of the lens and the proximal ends of the visual cells are enveloped in a dense layer of pigment forming the *iris* which is only interrupted by the fibres of the ocellar nerve.

2. THE LATERAL OCELLI. The lateral ocelli are, with very few exceptions, the only eyes present in insect larvæ. As their name implies, they are located on the sides of the head where they occupy positions corresponding with those of the compound eyes of the imagines. The number of lateral ocelli is variable and not always constant in the same species: in some groups there is a single ocellus present on either side, while in others there may be 6, 7 or more ocelli. They differ essentially from the dorsal ocelli from the fact that they are innervated from the optic lobes of the brain. There are also great variations in the structure of the lateral ocelli; in some insects they are highly evolved organs, resembling the dorsal ocelli, while in others they are little more than groups of a few sense cells. Many of the structural variations represent different degrees either of degeneration or of arrested development.

The absence of compound eyes in almost all larvæ is due to the development of these organs being delayed until the pupal stage. Their places are consequently taken by the lateral ocelli which are adaptive organs functional during the larval instars. Although the formation of the complete compound eyes is postponed until pupation a small number of ommatidia (vide p. 80) may be developed in some cases and function as larval ocelli.

The principal types of lateral ocelli are dealt with below.

(*a*) In larval Tenthredinidæ there is a single ocellus present on either side of the head. Structurally these organs are almost identical with the dorsal ocelli already described. Each consists of a biconvex lens and an underlying vitreous body formed by the elongated cells of the corneagen layer: the retina is formed of a number of retinulæ each composed of four cells with a typical 4-partite rhabdom (vide Redikorzew, 1900). Among larval Coleoptera (*Dytiscus, Hydrophilus, Acilius*) the lateral ocelli exhibit the same essential structure but differ in their more detailed features (Fig. 77).

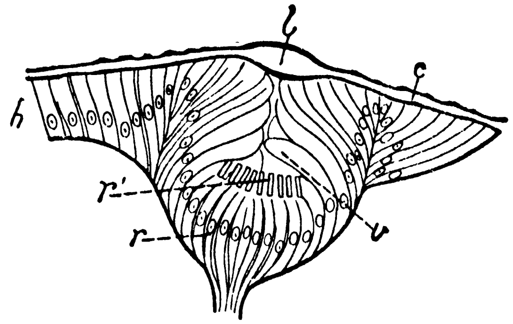

FIG. 77.—SECTION THROUGH AN OCELLUS OF A *DYTISCUS* LARVA.

c, cuticle; *l*, lens; *h*, hypodermis; *r*, retinal cells with their rhabdoms r^1; *v*, vitreous layer (modified hypodermal cells). *After* Grenacher.

(*b*) Among certain larval Lepidoptera and Trichoptera, and also in the larvæ of *Sialis*, *Myrmeleon* and certain other insects, each lateral ocellus has the general structure of a single ommatidium of a compound eye (Pankrath, 1890: Hesse, 1901).

(*c*) Among the Collembola the lateral eyes form the visual organs of the adults. They are variable in number, there often being 8 to a side, and each eye consists of a single ommatidium of the eucone type. Among the Poduridæ, however, they are more degenerate and have lost the crystalline cone cells (Fig. 78, B).

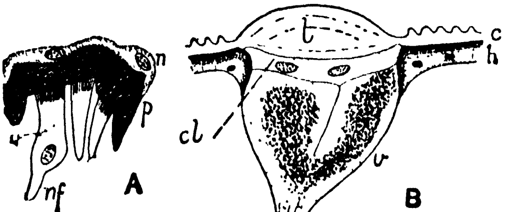

FIG. 78.—A. SECTION THROUGH AN EYE-SPOT OF A *CERATOPOGON* LARVA. *After* Hesse. B. SECTION THROUGH AN EYE OF *ANURIDA MARITIMA*. Original.

c, cuticle; *cl*, corneagen layer; *h*, hypodermis; *l*, lens; *nf*, nerve fibre; *p*, pigment cell and its nucleus *n*; *v*, visual cell.

(*d*) In many larvæ, particularly those living in partial darkness, the ocelli exhibit varying degrees of degeneration and, in *Ceratopogon*, they are reduced to a pair of visual cells with two overlying pigment cells (Fig. 78, A).

(*e*) In the larvæ of certain aquatic Nematocera (*Culex, Anopheles, Chaoborus, Dixa*, etc.) the lateral eyes are comparatively unimportant; the compound eyes, on the other hand, are present in varying degrees of development in close association with them, and eventually become transformed into the completed organs of the imago (vide Zavrel, 1907).

B. THE COMPOUND EYES

The principal feature distinguishing compound eyes from ocelli of either type is the fact that, in the former, the cornea is divided into a number of separate facets, whereas there is only a single facet to each ocellus. Compound eyes are formed of aggregations of separate visual elements known as ommatidia, each ommatidium corresponding with a single facet of the cornea. Certain other features have been regarded as distinctive of compound eyes, but in some cases they are also found in ocelli. Compound eyes, similarly to lateral ocelli, are innervated from the optic lobes of the brain (Fig. 81).

The number and size of the facets of the compound eye vary within wide limits. In extreme cases, as in the worker of the ant *Ponera punctatissima*, each eye is composed of a single facet. According to Forel there are 6–9 facets in the same caste of *Solenopsis fugax*, while among other ants the number varies between about 100 and 600 in the workers, 200 and 830 in the females, and between 400 and 1,200 in the males. In *Musca* the eye consists of about 4,000 facets, in some Lepidoptera from 12,000 to 17,000 (Packard) and in Odonata between 10,000 and 28,000 or more (Tillyard). In most insects the facets are very closely packed together and assume a hexagonal form, but in some instances, where they are fewer in number and less closely compacted, they are circular. The facets are not always of equal dimensions over the whole area of the eye. Thus, in the males of *Tabanus* they are often larger over the anterior and upper parts of the eye, but the two fields are not sharply demarcated. In the males of certain other Diptera, including species of *Bibio* and *Simulium*, the two areas of different sized facets are very distinctly separated, each eye appearing to be double (Fig. 79). The extreme condition is attained among certain Coleoptera (*Gyrinus*, several Cerambycidæ, etc.) and Ephemeroptera (*Chlœon*), where the two parts of the eye are so remote from each other that the insect appears to possess two pairs of compound eyes (Fig. 80). In *Chlœon* the anterior division of each eye is elevated upon a pillar-like outgrowth of the head, while the posterior division is normal.

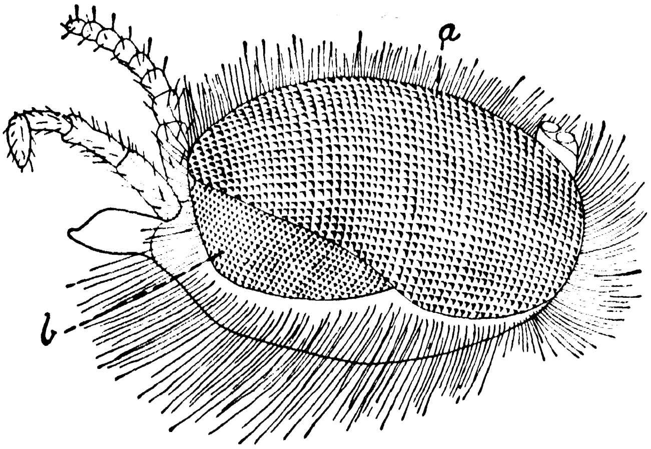

FIG. 79.—HEAD OF *BIBIO MARCI* (MALE), SHOWING DIVIDED EYE (LEFT).

a, upper division of eye ; *b*, lower division

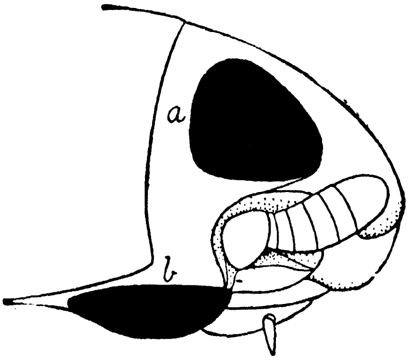

FIG. 80.—HEAD OF *GYRINUS NATATOR*, SHOWING DIVIDED EYE (RIGHT).

a, upper division of eye ; *b*, lower division.

THE STRUCTURE OF AN OMMATIDIUM (Fig. 82). The structure of the ommatidia varies in different insects but in all cases the differences are modifications of a common type. The various parts which enter into the composition of an ommatidium, passing from without inwards, are enumerated below.

(*a*) *The cornea.*—The cornea is the transparent area of cuticle forming the facet or lens of an ommatidium and is often more or less biconvex in form. It is cast off during each act of ecdysis.

(*b*) *The corneagen layer.*—The part of the hypodermis which extends beneath the cornea is known as the corneagen layer. It consists of two cells which, in some insects, are only to be detected with difficulty. In other cases they are wanting and, in these instances the cornea is secreted by the outer ends of the cells of the crystalline cone.

(*c*) *The crystalline cone cells.*—Beneath the corneagen layer or the cornea, as the case may be, there is a group of four cells which in the eucone eyes secrete a transparent body termed the *crystalline cone.* The nuclei of these cells are sometimes known as the nuclei of Semper.

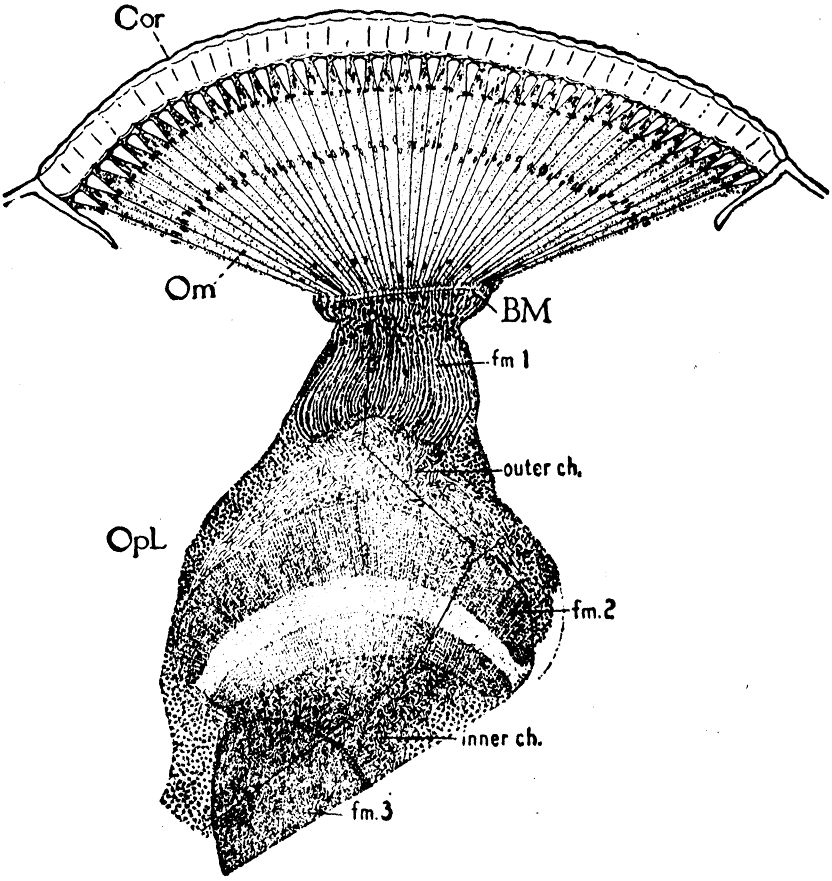

FIG. 81.—SECTION THROUGH THE EYE AND OPTIC LOBE OF A WORKER HONEY BEE.

BM, basement (or fenestrated) membrane; *Cor*, cornea; *fm_1*, perioptichon; *fm_2*, epiopticon; *fm_3*, opticon; *inner ch*, internal chiasma; *Om*, ommatidium; *OpL*, optic lobe; *outer ch*, external chiasma. From Snodgrass, *after* Phillips.

(*d*) *The primary iris cells.*—These are densely pigmented cells which are disposed in a circlet surrounding the cells of the crystalline cone and the corneagen layer.

(*e*) *The retinula.*—The retinula forms the basal portion of an ommatidium and is composed of a group of usually seven pigmented visual cells. Each of the latter is continuous with a post-retinal fibre and forms a nerve end cell. The visual cells collectively secrete an internal optic rod or *rhabdom* and the portion of the latter contributed by each cell is termed a *rhabdomere.* Each rhabdomere is stated to exhibit an extremely fine fibrillar structure, the individual fibrils passing right through the cell and emerging as the single nerve fibre previously alluded to. The rhabdom forms the central axis of the retinula and is in contact with the extremity of the crystalline cone.

(*f*) *The secondary iris cells.*—These are commonly elongated pigment cells which surround the primary iris cells and the retinula, thus serving to isolate an ommatidium from its neighbours.

The proximal extremities of the ommatidia rest upon a fenestrated or *basement membrane* through whose perforations pass the nerve fibres from the retinulæ and frequently fine tracheæ. The latter, as they enter further into the eye, become arranged parallel with the long axes of the ommatidia. The nerve fibres (post-retinal fibres) collectively unite the ommatidia with the periopticon or outermost tract of the optic lobe of the brain.

THE TYPES OF COMPOUND EYES.—Four types of compound eyes are described among insects. Of these, the first three were recognized by Grenacher (1879) and the fourth type by Kirchoffer (1908–10).

1. *Eucone eyes.*—In eyes of this type each ommatidium contains a true crystalline cone, which is a hard refractive body formed as an intracellular product of the cone cells: the nuclei of the latter are located in front of the cone. Eucone eyes are found in the Thysanura, Orthoptera, Odonata, Ephemeroptera, Trichoptera, Lepidoptera, Hymenoptera, Chrysopidæ, certain of the Hemiptera and in the Cicindelidæ, Carabidæ, Dytiscidæ and Scarabæidæ among Coleoptera.

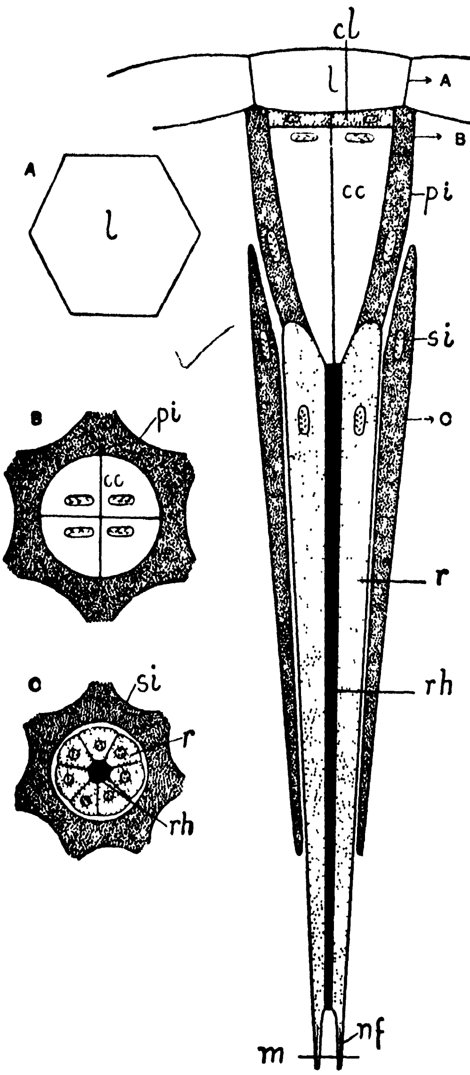

FIG. 82.—DIAGRAM OF GENERALIZED OMMATIDIUM OF THE EUCONE TYPE FROM AN EYE GIVING AN APPOSITION IMAGE.

cc, crystalline cone ; *cl*, corneagen layer ; *l*, corneal lens ; *m*, fenestrated membrane ; *nf*, nerve fibre ; *pi*, primary iris cell ; *r*, retinula ; *rh*, rhabdom ; *si*, secondary iris cells. A, B, and C, transverse sections of regions bearing corresponding lettering.

2. *Pseudocone eyes.*—In this type of eye there is no true crystalline cone and the four cone cells are filled with a transparent, semi-liquid material which lies in front of the nuclei. Pseudocone eyes are found in the Brachycera and Cyclorrhapha among Diptera.

3. *Acone eyes.*—In the acone eyes there is a group of elongate, transparent

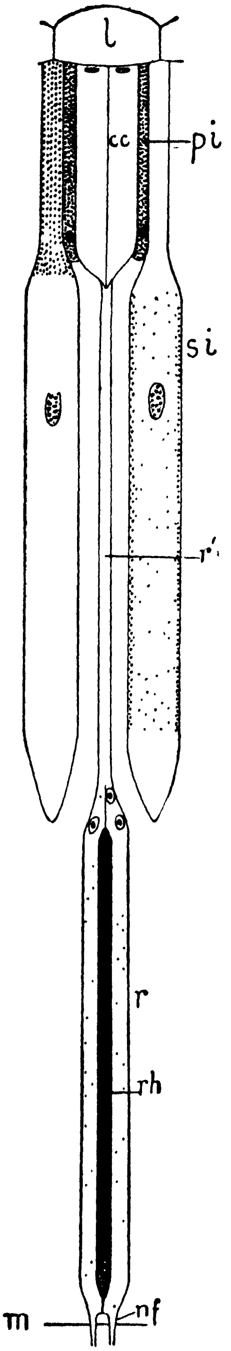

FIG. 83.—DIAGRAM OF AN OMMATIDIUM FROM AN EYE GIVING A SUPERPOSITION IMAGE.

On the left side the pigment is seen in a condition adapted for night vision and on the right side for day vision. r^1 filamentous prolongation connecting retinula with crystalline cone. Other lettering as in Fig. 82.

cone cells but the latter do not secrete any kind of cone whether crystalline or liquid. Eyes of this kind are found in the Dermaptera, Hemiptera, certain of the Diptera Nematocera, and in the Staphylinidæ, Histeridæ, Silphidæ, Coccinellidæ and Curculionidæ among Coleoptera.

4. *Exocone eyes.*—The name exocone is here applied to that type of eye in which the crystalline cone is replaced by a cone of extracellular, cuticular origin which appears as a deep ingrowth from the inner aspect of the corneal facet, in front of the unmodified cone cells. Eyes of this type are found in the Dermestidæ, Elateridæ, Byrrhidæ and Malacodermata (Kirchoffer).

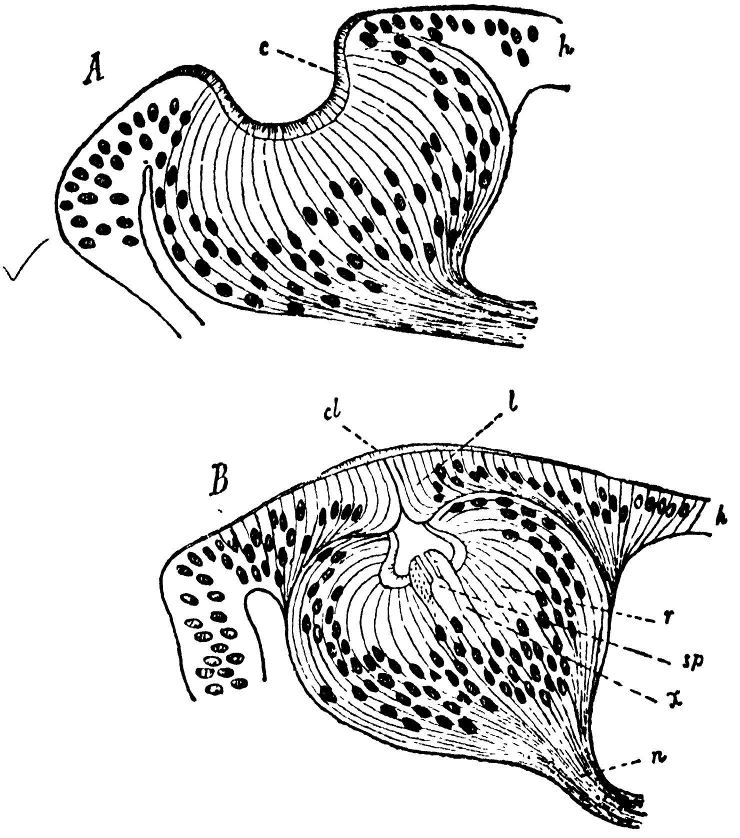

FIG. 84.—TWO STAGES IN THE DEVELOPMENT OF THE FIFTH OCELLUS OF AN *ACILIUS* LARVA (COLEOPTERA).

c, cuticular rods; *cl*, rudiments of lens; *h*, hypodermis; *l*, corneal layer (vitreous body); *n*, nerve; *r*, retina; *sp*, vertical slit in the retina; *x*, retinal cells bordering this slit. From Korschelt and Heider *after* Patten.

THE DEVELOPMENT OF EYES.—The structure of compound eyes and ocelli is best appreciated after taking into account the essential facts of their development (Figs. 84 to 87).

In the case of an ocellus development commences with the formation of a hypodermal pit. The cells bordering the edges of the pit become differentiated into the corneagen layer and vitreous cells: the deeper cells, forming the bottom of the pit, become grouped in such a manner as to produce the retinulæ, their inner ends giving off nerve fibres which unite to form the optic nerve. In the simple type of ocellus, exhibited in the larva of *Dytiscus* (Fig. 77), the mouth of the pit is still perceptible beneath the lens. In the larva of *Acilius* Patten has shown that the marginal cells of the pit grow inwards, and meet over the deeper parts, thus producing a two-layered ocellus. In the larva of *Hydrophilus* a more complex three-layered condition is arrived at by a fold of the hypodermis on one side of the pit (Fig. 86).

Each ommatidium of the compound eye commences as a pillar of thickened, elongated, hypodermal cells, the pillars being separated by undifferentiated tissues (Fig. 87). The cells of the pillars become differentiated into an outer series yielding the facets, crystalline cones and primary pigment cells, and an inner series producing the retinulæ. The hypodermis between the ommatidial pillars becomes transformed into the secondary pigment cells (vide Johansen, 1893).

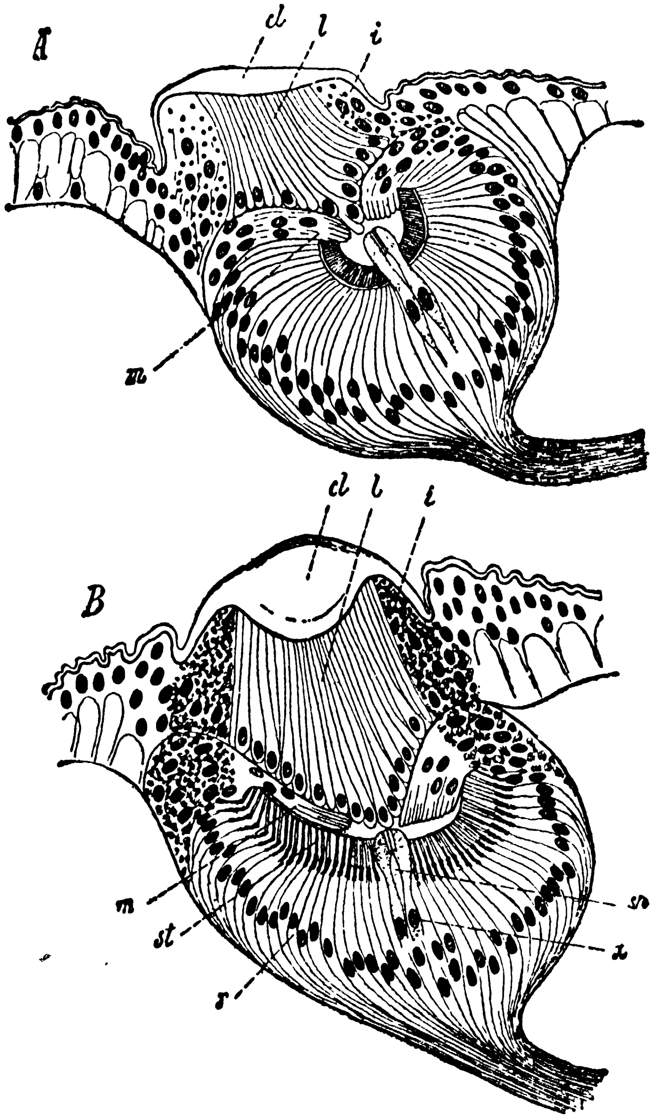

FIG. 85.—TWO LATER STAGES IN THE DEVELOPMENT OF THE FIFTH OCELLUS OF AN *ACILIUS* LARVA.

i, pigmented iris ; *m*, middle inverted layer of the eye ; other lettering as in Fig. 84. From Korschelt and Heider *after* Patten.

THE RELATIONS OF COMPOUND EYES TO OCELLI.—It is well known that very similar types of eye occur in distantly related animals, and that nearly allied species frequently differ in the fundamental structure of their visual organs. Even very different types of eye may occur in the same animal. In considering the relations of compound eyes to ocelli in insects the above facts, therefore, need to be borne in mind.

The lateral ocelli of many Collembola, and of larval Lepidoptera, are comparable individually with a single ommatidium of the compound eye.

In these instances the ocelli represent a few disseminated ommatidia or, in other words, they are rudiments of compound eyes. With the dorsal ocelli, and the lateral ocelli of a similar character, the case is very different. In organs of this kind there is a single lens in front of a larger or smaller number of retinulæ. In the compound eye there is a number of separate lenses or facets each associated with a single retinula.

Attempts have been made to derive the compound eye from an organ composed of a group of ocelli of this latter type. This method of origin is upheld by Korschelt and Heider whose conclusions are based upon a comparative study of the eyes of Myriapods. The eye of *Scolopendra* consists of a few typical ocelli, each with a cuticular lens: in *Lithobius* and *Julus* there are 30–40, or more, similar ocelli on either side. In *Scutigera* a kind of compound eye is present which is formed of 200, or more, closely compacted ocelli. The latter are considerably modified by mutual compression until they have assumed somewhat the character of ommatidia, the retinulæ associated with each ocellus being greatly reduced in number. This type of eye is regarded by Rosenstadt as intermediate between ocelli and true compound eyes.

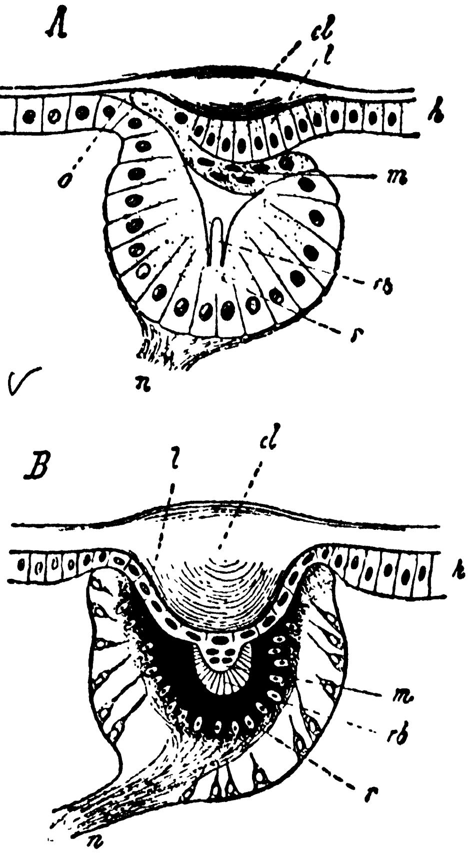

FIG. 86.—TWO STAGES IN THE DEVELOPMENT OF AN OCELLUS OF A LARVAL *HYDROPHILUS*.

cl, lens; *h*, hypodermis; *l*, corneagen layer; *m*, middle layer of optic rudiment; *n*, nerve; *o*, aperture of optic invagination; *r*, retinal layer; *rb*, rods. From Korschelt and Heider *after* Patten.

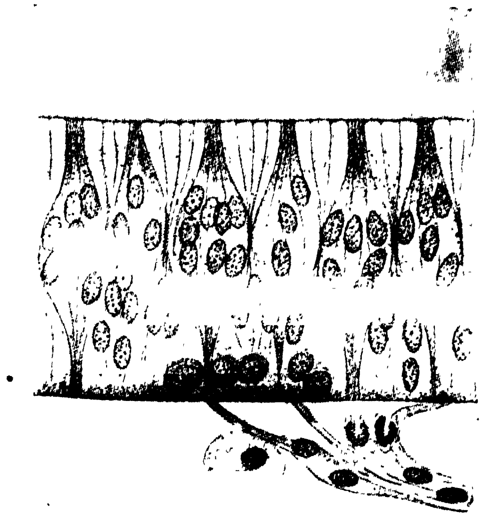

FIG. 87.—STAGE IN THE DEVELOPMENT OF THE COMPOUND EYE OF THE PUPA OF *SATURNIA PERNYI* SHOWING OMMATIDIAL PILLARS. *After* Bugnion and Popoff.

Grenacher regards ocelli and compound eyes as "sisters" derived from an ancestral type of visual organ, resembling an ommatidium of the acone type of the Tipulidæ. The compound eye is derived through an increase in the number of these simple eyes and their close aggregation; the ocellus is derived through the multiplication of the retinulæ with a corresponding increase in the size of the lens.

Insects alone afford no clue to the problem and speculations, confined within the limits of that class, lead only to the conclusion that if the two types of organs have a common origin that origin must be sought for elsewhere.

C. THE PHYSIOLOGY OF VISION

The eyes of insects, when completely developed, are divisible into two regions which are structurally and physiologically different. In the typical ocellus the corneal lens and vitreous cells constitute the dioptric portion of the eye, while the retinulæ along with their rhabdoms form the retina or percipient portion. In the compound eye the dioptric portion is composed of the corneal facets and the underlying layer of crystalline cones : the percipient portion is similarly composed of the retinulæ and their rhabdoms. The retina in insects is only comparable with the rod and cone layer of the retina of the vertebrate eye.

VISION BY MEANS OF OCELLI.—The dorsal ocelli are constructed upon a plan more nearly resembling that of the human eye than the Arthropod compound eye. Since there is no power of accommodation in the dioptric layer, and the lens is strongly biconvex, vision is limited to the perception of very near objects. The small number of visual elements implies an image of a crude or indefinite kind, and this image is an inverted one. The experiments of Plateau and others have shown that caterpillars, for example, do not perceive objects at a distance greater than 1 or 2 cm. : spiders, with their highly developed ocelli, have little power of appreciating the shapes of the objects which they see. Forel and Lubbock believe that the ocelli of the social Hymenoptera are used by those insects when in the darkness or subdued light of their nests. In a few words it may be said that experimental evidence indicates that ocelli are used to distinguish between light and darkness, and are capable of conveying a coarse image of very near objects only.

VISION BY MEANS OF COMPOUND EYES.—The principal theory accounting for vision by means of compound eyes is the well-known mosaic theory formulated by Müller in 1826. This explanation with certain modifications based on the work of Exner and others, is generally accepted to-day. Müller's views are best understood by regarding the compound eye as being built up of an immense number of minute, elongate, transparent tubes arranged with their long axes parallel to one another. Let each tube be coated externally with a dark pigment, so that it is optically isolated from its fellows, and the only rays of light which will traverse the tubes, from end to end, are those parallel with the long axes : oblique rays will impinge on the walls of the tubes and become absorbed by the pigment (Fig. 88). In the compound eye each ommatidium will only convey to the retinulæ rays coming from a very small portion of the whole field of vision, and only those travelling in the direction of its axis. The impression received through such an eye would be a single mosaic picture, formed by the same number of points of light as there are ommatidia, each point of light corresponding in colour and density to the corresponding part of the object viewed.

It is now generally recognized that compound eyes are specially adapted for perceiving the movement of objects. The movements of even a very small object in the field of vision would be immediately registered on the mosaic picture received on the retina, which would become suddenly altered in one or more of its components. The extent of the alteration would depend upon the size and distance of the object, and the number of ommatidia affected. Such movement would be quickly impressed upon the brain of the insect and the latter would respond accordingly. It is often possible to approach an insect so gradually that the change of position passes unnoticed. An object as large as a human being affects all the ommatidia equally and simultaneously and, since it is moving very slowly, the change of position only causes slight changes in the character of the image as a whole. A sudden slight movement of any part of the body is often sufficient to cause the insect's immediate departure, owing to the fact that it abruptly affects a series of ommatidia in succession.

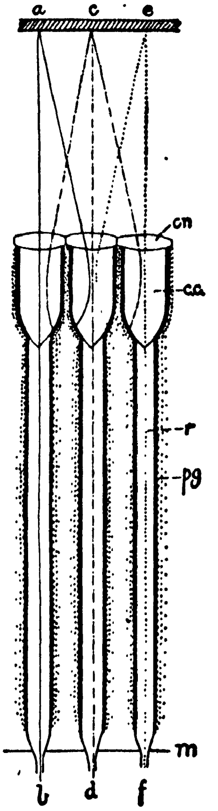

FIG. 88.–DIAGRAM REPRESENTING VISION WITH AN EYE GIVING AN APPOSITION IMAGE.

The only rays of light from an object *a c e* which will reach the retinulæ are those parallel to the long axes of the ommatidia (e.g. *ab*, *cd*, *ef*). All oblique rays impinge on the sides of the cones where they are absorbed by the pigment. *cn*, corneal lens; *c,c*, crystalline cone; *r*, retinula; *pg*, pigment; *m*, fenestrated membrane. This Fig. and Fig. 89 are based on Exner.

The distinctness of vision depends partly upon the number and size of the ommatidia. An image formed by a vast number of minute ommatidia will be sharper and more detailed than one formed by a smaller number of larger elements. It further depends upon the amount and distribution of the pigment surrounding each ommatidium, which determine the degree of isolation of the light passing through the latter. Since compound eyes generally possess no focussing mechanism, insects cannot perceive form beyond a few feet away, although perception of movement extends to a much greater distance. The closer an object is to the eyes the greater will be the number of ommatidia employed to produce the impression, and consequently the sharper the vision.

In eyes adapted solely for diurnal vision the retinulæ are in contact with the apices of the crystalline cones (Fig. 88). A dense layer of pigment surrounds the cones and only rays of light issuing from the apices of the latter reach the rhabdoms. An image formed in this kind of eye is termed an *apposition image* because it is built up of apposed points of light; it is a true mosaic in the sense of Müller. According to Exner the image produced is an inverted one, but apparently this is not always the case since Eltringham (1919) has observed an erect image in the eucone eye of a butterfly.

In eyes of many nocturnal and crepuscular insects the rhabdoms are not in contact with the apices of the cones, the two elements being separated by a space filled with transparent tissue. The ommatidia in this kind of eye are consequently greatly elongated (Fig. 89). The pigment is capable of forward or backward migration according to the amount of light available. At night time it moves forward and freely exposes a large portion of the cone apices with the result that rays of light entering adjacent ommatidia, traverse the space already alluded to and reach the same retinula. In this type of eye there is an overlapping of points of light and the image thus formed is termed by Exner a *superposition image*, which is an erect one. It is evident that in an eye of this description a limited amount of light will produce a better image than in an eye giving an apposed image where much of the light is absorbed by the pigment. The eyes of nocturnal insects are adapted, therefore, to perceive the general forms and the movements of objects when there is very little light available. Owing to the overlapping previously explained the image is a continuous one and not a true mosaic. Many insects with eyes giving superposition images are adapted to make the most of varying degrees of light. In the presence of an increased amount of light the pigment moves backwards, like a dark sleeve cutting off more and more of the peripheral rays and, in this manner, the luminosity of the image is decreased without reducing its clearness. By fixing and sectioning the eye of an insect which had been kept for a time in the light, and comparing it with the eye of another individual of the same species which had been confined in the dark, Exner was able to definitely prove that corresponding changes in the distribution of the pigment take place.

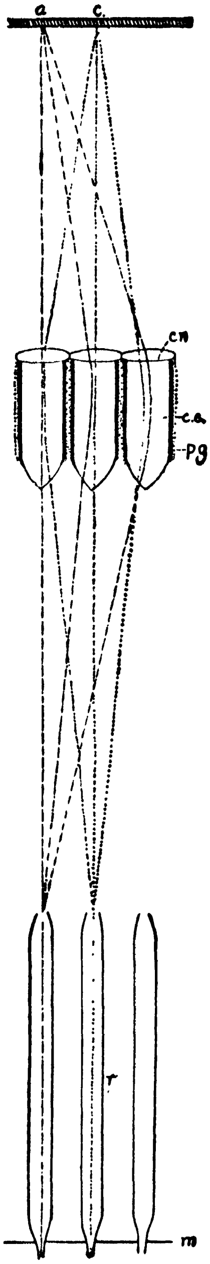

FIG. 89.—DIAGRAM REPRESENTING VISION WITH AN EYE GIVING A SUPERPOSITION IMAGE.

Each retinula receives not only an image from rays entering its own facet, but also those from peripheral oblique rays from neighbouring facets. Lettering as in Fig. 88.

In night-flying insects there is a structure termed the *tapetum* which reflects the light that has entered the eyes causing the latter to shine in the dark, when they assume the appearance of golden or ruby globes. In eyes of this kind the retinular elements are impregnated with a special colouring substance (erythropsin, zanthopsin) and the spaces between the retinulæ are densely packed with fine, longitudinal tracheæ filled with air (Fig. 90). It is probable that the effect of the faint nocturnal light is intensified owing to the light passing through the retinulæ a second time, when it is reflected from the glistening tracheæ of the tapetum (vide Bugnion and Popoff, 1914).

The divided eyes of certain insects have been alluded to on a previous page. Such eyes consist of an upper portion composed of large facets, which are adapted to give a superimposed image, and a lower portion composed of smaller facets giving an apposed image. The upper part of such an eye is probably used to perceive variations in the intensity of light from above produced by clouds, moving enemies, etc., without there being any necessity to perceive definite form. The lower part of the divided eye is clearly adapted for more acute vision, and to receive the more exact impressions produced by the objects over which the insect may be flying or resting. In some cases possibly the larger facets may also function for night vision and the small facets for day vision. For a fuller account of insect vision reference should be made to the recent manual by Eltringham (1933).

Recent research on the responses of insects to light tend to the conclusion that they are able to distinguish between differences of wave-length or colours. In the honey bee indirect evidence is derived from the experiments of von Frisch (1914) who conditioned bees to associate certain colours with food. He also found that these insects were unable to distinguish between red, black or grey and his main results were confirmed by Kühn (1927). The latter observer concluded that since bees did not respond to rays over 650$\mu\mu$ they were red-blind, and he also showed that they responded to ultra-violet rays down to at least 313$\mu\mu$. Bertholf (1931), who took means to equalize the intensity of the rays employed, added direct evidence to the theory that colour vision exists in insects: he also concluded that the upper limit of spectral responses in the bee reaches to at least 677$\mu\mu$ in the red region. The lower limit for a number of insects is in the ultra-violet region, and Lutz (1924) found that insects, in confinement, will fly to the apparently opaque ultra-violet screen as though it were clear glass and attempt to escape. According to Bertholf (1931A) bees respond to the ultra-violet rays down to a wave-length of 297$\mu\mu$ with a maximum response at about 365$\mu\mu$. This experimenter found that the stimulative efficiency at the latter wave-length is about 4·5 times as great as that of the yellow-green (553$\mu\mu$) which he found to be the most effective region in the so-called visible spectrum.

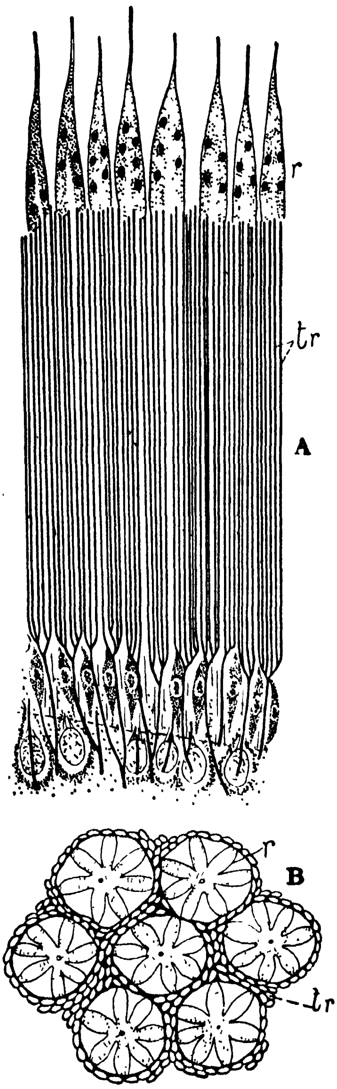

Fig. 90.—A. Retinulæ of the Eye of *Deilephila euphorbiæ*, showing Groups of Fine Longitudinal Tracheæ. B. Transverse Section of a Group of Retinulæ of the Eye of *Phlogophora meticulosa*, showing the Interspaces packed with Tracheæ.

tr, tracheæ; *r*, retinulæ. *After* Bugnion and Popoff.

4. The Chordotonal or Auditory Organs

It is well known that many insects are capable of sound production, and the possession of organs for this purpose indicates the probability that they also possess some mechanism for sound perception. Structures that are believed to fulfil the latter function exist in a number of insects, even in their larval stages, and are known as chordotonal or auditory organs. They consist typically of spindle-shaped bundles of sensillæ, or *scolophores*, whose distal extremities are usually attached to the integument: less frequently they are without this attach-

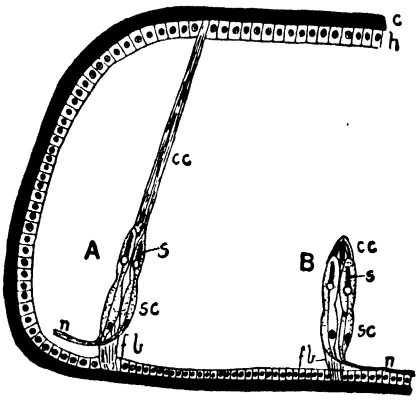

Fig. 91.—Diagram of the Two Types of Scolophores.

A, integumental; B, subintegumental. *c*, cuticle; *h*, hypodermis; *cc* cap cell; *s*, scolopale; *sc*, sensory cell; *fb*, fibrillar binding tissue; *n*, nerve.

ment and end tree in the body-cavity. The two types may be distinguished respectively as the *integumental scolophores* and the *subintegumental scolophores* (Fig. 91).

In the most completely developed chordotonal organs the sensory parts are covered over by a special thin area of the integument, which forms an external vibratory membrane or *tympanum* and, for this reason, they are often termed *tympanal organs*.

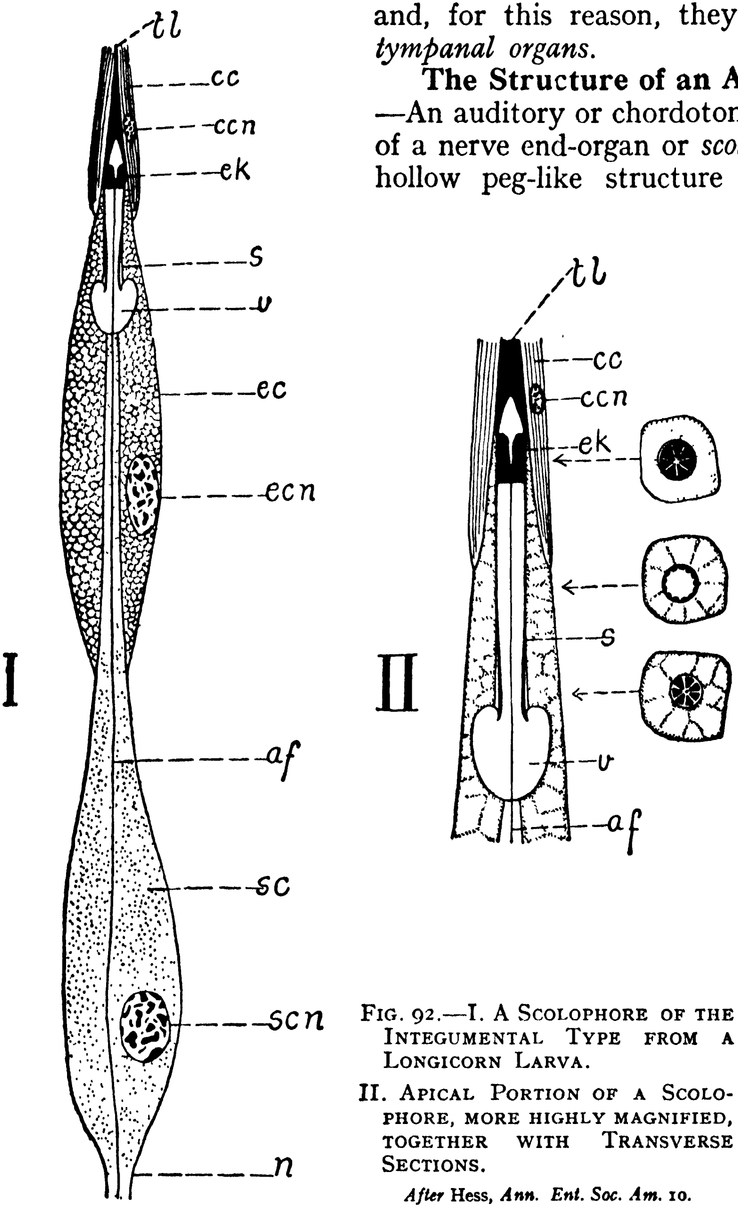

Fig. 92.—I. A Scolophore of the Integumental Type from a Longicorn Larva.

II. Apical Portion of a Scolophore, more highly magnified, together with Transverse Sections.

After Hess, *Ann. Ent. Soc. Am.* 10.

af, axial fibre ; *cc*, cap cell ; *ccn*, nucleus of cap cell ; *ec*, envelope cell and its nucleus *ecn* ; *ek*, end knob ; *n*, nerve fibre ; *s*, scolopale ; *sc*, nerve end-cell and its nucleus *scn* ; *tl*, terminal ligament ; *v*, vacuole.

The Structure of an Auditory Sensilla.—An auditory or chordotonal sensilla consists of a nerve end-organ or *scolophore*, enclosing a hollow peg-like structure or *scolopale* (vide Schwabe 1906). A scolophore (Fig. 92) is composed of a bipolar nerve end-cell, continuous proximally with a fibre of the chordotonal nerve. This sensory cell is drawn out distally into a slender prolongation, which is enclosed by an *envelope cell* and a *cap cell*. The scolopale is formed within the envelope cell and its cavity communicates basally with a vacuole filled with a watery fluid. Viewed in transverse section the wall of the scolopale is composed of a number of ribs : in the simple type of chordotonal organs studied by Hess (1917) there are seven of these ribs at either end of the scolopale, each of which is divided in the central portion so that there are fourteen ribs in this part. The distal end of the scolopale is almost always thickened to form the *end-knob*. The entire scolopale is bathed by a fluid medium in which it is free to vibrate. The cap cell appears to be a modified hypodermal cell and, in a scolophore of the integumental type, it forms a greatly elongated strand which serves to attach the sensilla to the body-wall. An axial fibre, or a group of neurofibrils, from the chordotonal nerve traverses the whole length of the sensory cell and scolopale to join the end-knob of the latter.

The Simpler Type of Chordotonal Organs.—The scolophores rarely exist as single sensillæ, usually two or more are disposed closely together in a chordotonal organ. Those studied by Hess in Cerambycid larvæ are individually composed of four scolophores. Each organ is in the form of a minute ligament which is attached to the integument at one extremity by the elongated cap-cells, alluded to previously, and at the other extremity by a short strand of connective tissue. The latter forms the fibrillar binding substance of Schwabe, and is prolonged over the scolophores sô as to ensheath them.

Graber (1882–83), who laid the foundation of existing knowledge of the chordotonal organs, found them in all the larger orders of insects. They are not always located in the same region of the body, their positions often varying in different groups. In ants, for example, they are commonly found in the tibiæ, but Janet has discovered a number of less conspicuous organs of a similar nature, in various parts of the body, numbering eight pairs in all. Chordotonal organs also occur on the tibiæ in certain termites and Perlids, and in the tarsi in some Coleoptera.

In addition to adult insects chordotonal organs have been observed in many larvæ including those of *Dytiscus*, *Melolontha*, and the Cerambycidæ among Coleoptera: *Tabanus*, *Chaoborus*, *Chironomus* and *Syrphus* among Diptera: in *Carpocapsa* among Lepidoptera and *Nematus* among Hymenoptera. As a rule there is a pair of these organs in most of the abdominal segments and they are innervated from the ganglia of the ventral nerve cord (Fig. 93); in *Dytiscus* and *Melolontha* they are located in the tarsi.

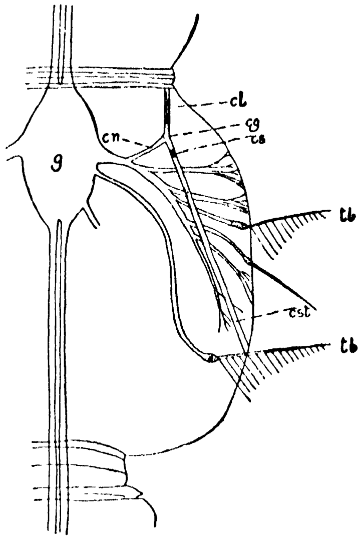

FIG. 93.—RIGHT HALF OF 8TH BODY-SEGMENT OF THE LARVA OF *CHAOBORUS*.

cg, *cs*, chordotonal organ and its terminal prolongation *cst*; *cl*, basal ligament; *cn*, chordotonal nerve; *tb*, tactile setæ; *g*, ganglion of ventral nerve cord. *After* Graber.

The Tympanal Organs.—Highly specialized auditory organs are found in the Acridiidæ on either side of the first abdominal segment (vide Schwabe, 1906; Baier, 1930). They are easily recognized by the presence of a tense, external vibrating membrane or *tympanum*, which is surrounded by a horny ring (Figs. 94, 95). A group of numerous scolophores, forming a swelling known as *Müller's organ*, is applied to the inner surface of each tympanum, and forms the termination of the auditory nerve which arises

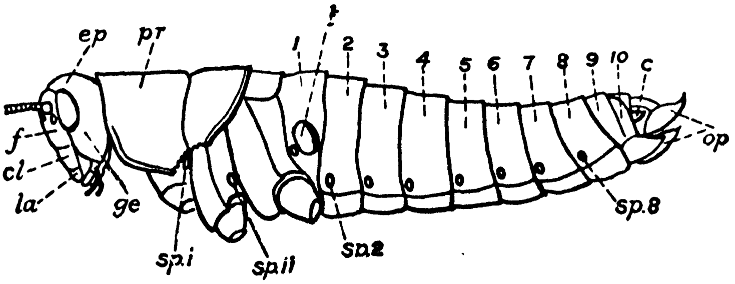

FIG. 94.—LATERAL VIEW OF A LOCUST WITH WINGS AND LEGS REMOVED SHOWING TYMPANUM *t*.

After Carpenter.

from the metathoracic ganglion. Two horny processes and a delicate pyriform vesicle, which is filled with a clear fluid, are intimately associated with Müller's organ ; they probably serve to transmit the tympanal vibrations to the sensillæ. The first abdominal spiracle is located near the anterior margin of the tympanum, and it gives off an air-sac which is applied to the under surface of that membrane : two other air-sacs take their origin in the second abdominal segment, from the ventral tracheal trunk of their side, and lie internal to and in close contact with the air-sac first mentioned.

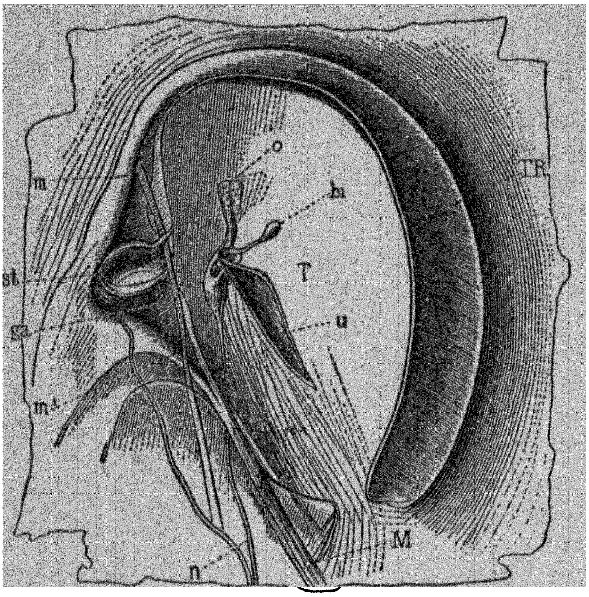

Fig. 95.—Tympanum of a Locust (*Caloptenus*) viewed from Within.

T, tympanum with its border TR ; *bi*, pyriform vesicle ; *o*, *u*, horn-like processes ; *ga*, Müller's organ ; *n*, auditory nerve ; *st*, spiracle ; *M*, tensor muscle of tympanum. *After* Graber.

In the Tettigoniidæ and Gryllidæ there is often a pair of tympanal organs near the proximal extremity of the tibia of each fore-leg (Fig. 96). In many genera these structures are easily observable, but, in certain others, each organ is concealed by an integumental fold and comes to lie in a cavity: the latter communicates with the exterior by means of a slit-like opening.

These organs attain great complexity of structure and most of what is known concerning them is due to the researches of Graber (1876), von Adelung (1892) and Schwabe. In *Deticus verrucivorus* the tympanal organs are of the concealed type (Figs. 97 and 98). The trachea supplying the leg is greatly modified and, on entering the tibia, it becomes inflated and divides into an anterior and a posterior branch, which reunite below the auditory organ. Each trachea is closely applied to the tympanum of its side, which thus has air on both its aspects: the open air on the outer surface, and the air of the trachea on its inner surface. It is noteworthy that these tracheæ communicate with the exterior by a special orifice on either side, in close proximity to the prothoracic spiracle, and these orifices are only present in species with tympanal organs. In a transverse section of the tibia (Fig. 98) it will be observed that the two tracheæ occupy the area between the tympana. There is an extensive outer chamber in the leg (above the tracheæ as seen in the figure) and a corresponding inner chamber below. The outer chamber contains the supra-tympanal organ together with leucocytes and adipose cells. The *supra-tympanal organ* is placed a short distance above

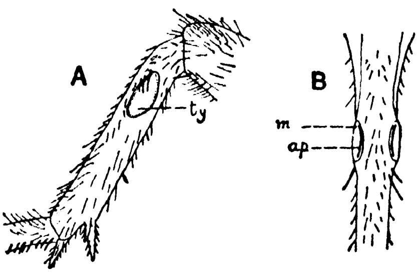

Fig. 96.—Left Fore-Tibia of *Gryllus domesticus* seen from the Outside showing Tympanum *ty*.
B. Portion of Fore-Tibia of *Locusta viridissima*, frontal view.

m, membrane covering tympanum ; *ap*, aperture into tympanal chamber.

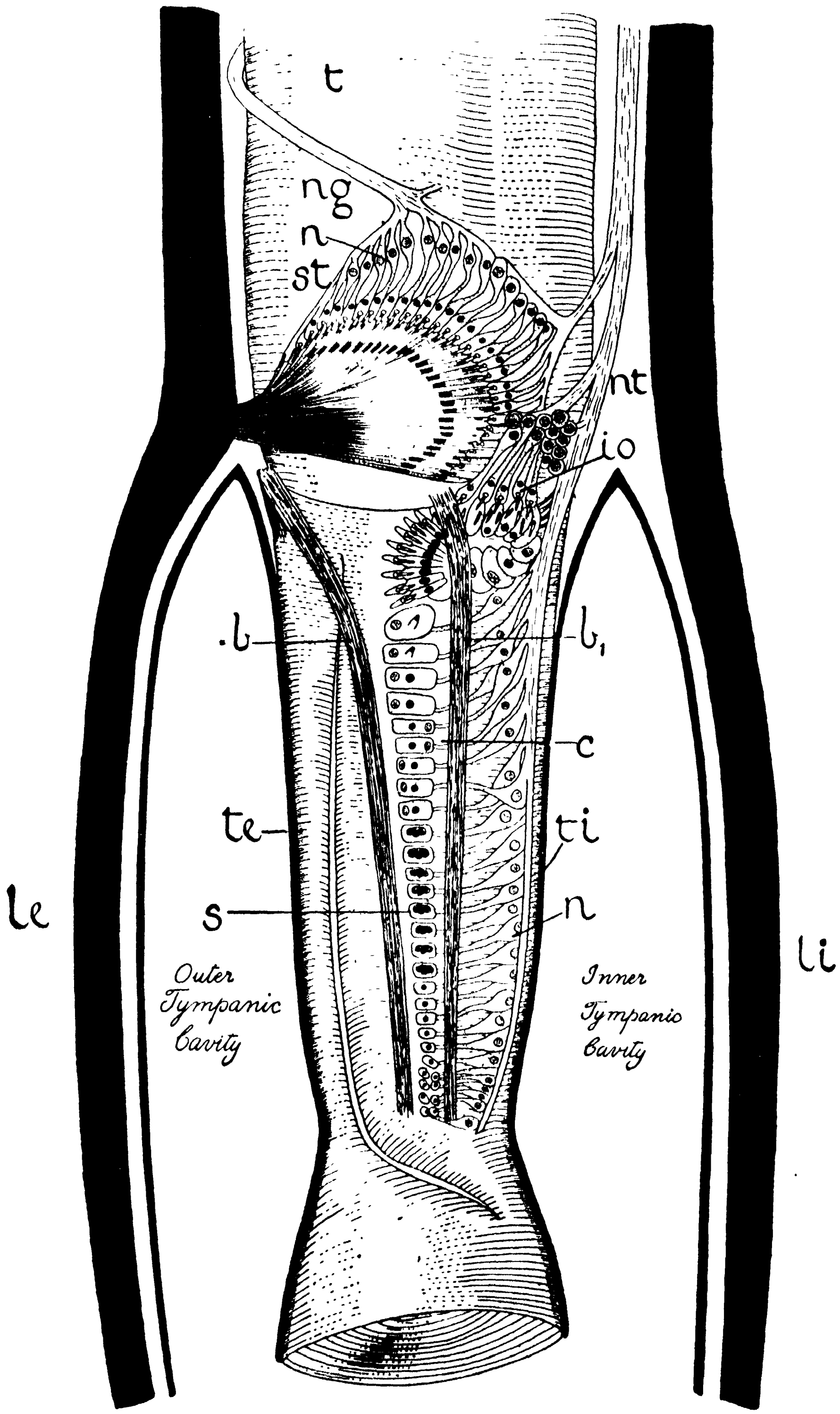

FIG. 97.—LONGITUDINAL SECTION OF THE FORE-TIBIA OF *DETIOUS.*

c, crista acustica with its supporting bands *b* and b_1; *io*, intermediate organ; *le*, *li*, outer and inner aspects of tibia; *n*, nerve cells; *ng*, subgenual branch of crural nerve; *nt*, tympanal nerve; *s*, scolopalæ; *st*, supra tympanal organ; *t*, main trachea; *te*, *ti*, outer and inner tympana. Redrawn from Schwabe, *Zoologica*, 1906.

the tympana, and is composed of a number of scolophores of the integumental type, whose cap cells are attached to the integument of the leg. Immediately below this organ, on its outer side, there is a smaller sensory structure which is termed the *intermediate organ* : it is composed of scolophores of the subintegumental type. On the outer face of the anterior trachea is a third chordotonal organ—the *crista acustica* (*organ of Siebold*). It is an elongated ridge or crest composed of a large number of scolophores of the sub-integumental type, which gradually decrease in size towards the distal extremity of the tibia. There are two principal nerves in the tibia —the tibial nerve and the tympanal nerve,—both arising from the prothoracic ganglion. The supra-tympanal organ is supplied by a branch from each of those nerves, while the two remaining organs are innervated by the tympanal nerve.

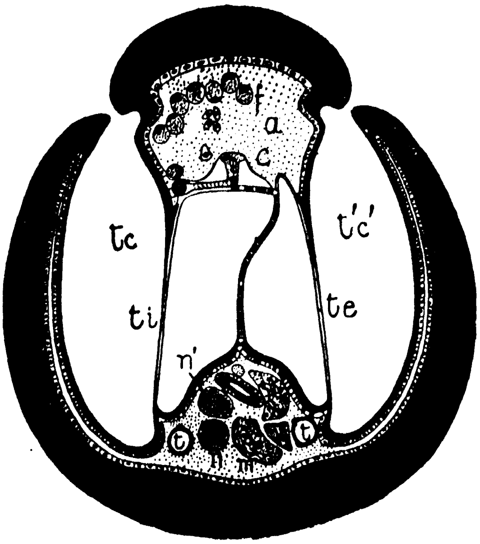

FIG. 98.—TRANSVERSE SECTION OF THE FORE-TIBIA OF *DETICUS* PASSING THROUGH THE CRISTA ACUSTICA (*c*).

a, anterior blood space ; *f*, fat-body ; *m*, muscles ; *n*, tarsal nerve ; *n*¹, tibial nerve ; *t*, tracheæ ; *tc*, *t*¹*c*¹, inner and outer tympanic cavities ; *ti*, *te*, inner and outer tympana. Redrawn from Schwabe.

Tympanal organs also occur in individuals of both sexes in Cicadidæ. In these insects Vogel (1923) has shown that the cavity of the operculum of the sound-producing organ is bounded posteriorly by a true tympanum named the "mirror." The percipient part of this organ consists of a group of about 1,500 chordotonal sensillæ stretching like a ligament across a kind of auditory cavity. Vogel considers that, owing to the much greater length of these sensillæ as compared with the elements composing the organ of Corti in man, cicadæ are only capable of appreciating a limited range of sound waves. In many families of Lepidoptera conspicuous tympanal organs are also present on either side of the metathorax or at the base of the abdomen. These organs have been chiefly investigated by Eggers (1919) and by Kennel and Eggers (1933). Each organ consists of an internal vesicle invested by tracheal epithelium and lodged in a cavity formed by an

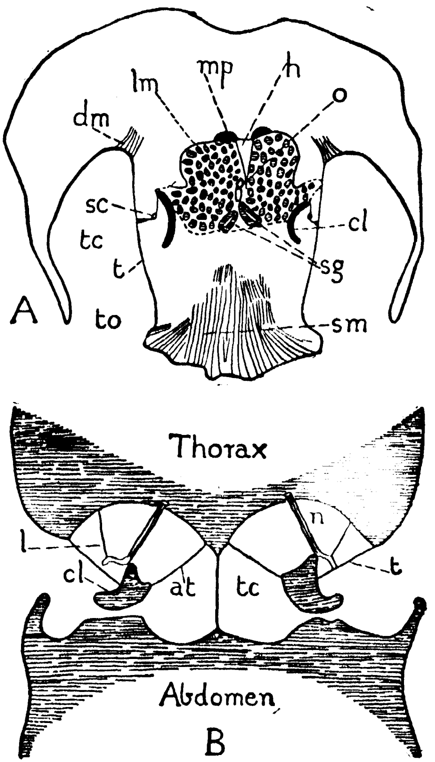

FIG. 99.—TYMPANAL ORGANS OF LEPIDOPTERA. A. VERTICAL SECTION ACROSS BASE OF ABDOMEN OF A GEOMETRID MOTH. B. A DIAGRAMMATIC HORIZONTAL SECTION ACROSS BASE OF THORAX AND ABDOMEN OF A NOCTUID MOTH.

at, accessory tympanum ; *cl*, cuticular lamella ; *dm*, dorsal muscle of tympanum ; *h*, heart ; *l*, ligament supporting chordotonal organ ; *lm*, longitudinal muscles ; *mp*, mesophragma ; *n*, chordotonal nerve ; *o*, œsophagus ; *sc*, scolopalæ ; *sg*, salivary gland ; *sm*, sternal muscles ; *t*, tympanum ; *tc*, tympanic chamber ; *to*, external opening of tympanic chamber. Adapted from Eggers and v. Kennel.

invagination of its segment. The cavity communicates with the exterior of an opening which is guarded by an integumentary fold. Just within the opening is the glistening tympanic membrane and, closely associated with it, is a pair of chordotonal sensillæ connected with a special tympanic nerve from the metathoracic ganglion. Whereas in Geometrid moths the tympanal organs are lodged in the abdomen, in Noctuid moths they are situated in the thorax and, lying more deeply within the tympanic vesicle, there is an accessory tympanum which appears to function as a resonator (Fig. 99). Experiments by Eggers showed that moths possessing these organs respond to sounds by wing movements or by flight. When both tympana are destroyed such responses ceased.

Tympanal organs are described by Hagemann (1910) in *Corixa* and its allies on either side of the mesothorax, in close relation with the second pair of spiracles.

Johnston's Organ.—The organ which has received this name was first recognized in 1855 by Christopher Johnston and has since been observed in representatives of most of the larger orders of insects (vide Child 1894: also Eggers 1928). It is located within the second antennal joint, and presents a certain amount of variation in form and degree of development in different insects, and in the two sexes of the same species. The organ attains its greatest complexity among male Culicidæ and Chironomidæ: it is also tolerably well developed in such diverse insects as *Calliphora*, *Vespa*, and *Satyrus*. Viewed in section it is composed of a variable but considerable number of sensillæ, which usually surround the antennal sensory nerve where it passes through the particular joint (Fig. 101). The sensillæ only differ slightly from those of the chordotonal organs and also contain scolopalæ. Their distal extremities are attached to a process of the conjunctival plate, between the 2nd and 3rd joints of the antenna, and their proximal ends are continuous with fibres of the antennary nerve. It has been shown experimentally by Mayer (1874) that the whorls of setæ on the 3rd and following antennal joints are caused to vibrate by different notes, being most affected when at right angles to the direction from which the sound came. It is believed that vibrations of the antennal setæ are transmitted to the conjunctival plate, and thence to the sensillæ, and that insects possessing these organs are able to appreciate sounds produced by their own species.

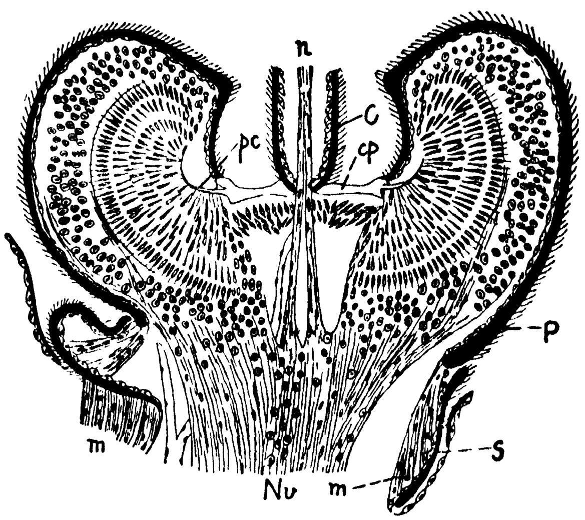

FIG. 100.—LONGITUDINAL SECTION OF THE BASE OF THE ANTENNA OF A MALE MOSQUITO (*CHAOBORUS*) SHOWING JOHNSTON'S ORGAN.

s, scapa; *p*, pedicel; *cp*, conjunctival plate and its process *pc*; *C*, base of clavola; *Nv*, antennary nerve; *n*, nerve to clavola; *m*, antennal muscles. *After* Child, 1894

The Physiology of the Chordotonal Organs.—In the simpler types of chordotonal organs, and in various tympanal organs already described, it is believed that sound waves impinge on the overlying body-wall, and the stimulus is transmitted to the scolopalæ which respond to a corresponding degree, since they are free to vibrate in the fluid surrounding them. Probably, by altering the tension of these ligament-like organs, they can be "tuned up" as it were, to appreciate a considerable range of vibrations. Eggers (1919) claims that the chordotonal organs function in coördinating movements of the appendages and wings, also those concerned with respiration and the heart pulsations. Such muscular activities, he states, are largely rhythmic and are regulated by means of these sensillæ. In the case of the tympanal organs it will be observed, from the preceding account, that the tympanal membrane is maintained in a condition of equilibrium by means of air-pressure exerted on both sides of it, the closely connected trachea acting very much like the Eustachian tube in the human ear. Sound waves impinging on the tympanum cause the latter to vibrate, and these vibrations appear to be transmitted to the nerve concerned by one of two methods. Since the scolophores in the crista acustica are turned away from the tympanum, the vibrations have either to act on the air in the tracheæ, or on the fluid in the anterior chamber of the leg, in the first instance, and indirectly affect the scolophores: in the Acridiidæ the tympanal vibrations appear to be directly transmitted to the scolophores.

5. Other Sense Organs, Including Those of Unknown Function

In addition to the various kinds of sensillæ described in this chapter there is a widely distributed type variously known as the *campaniform sensillæ*, sense domes or olfactory pores (Fig. 101). Each consists of a thin, and commonly dome-like, cuticular structure overlying a large pore-canal: it may either project from the general surface of the integument, or be deeply enclosed in a cavity of the latter. In sectional view it is seen to be traversed by a nerve fibre which terminates in a scolopala attached to the inner surface of the cuticular covering. These campaniform sensillæ were discovered by Hicks (1857) and have been since studied by Vogel (1911), McIndoo (1914), Sihler (1924) and others. They occur distributed over many parts of the body, wings, halteres, antennæ, sting and other organs in insects of various orders. Many hypotheses have been advanced as to their function. McIndoo claims that the covering membrane is perforated by a minute pore which allows of the nerve ending to come in direct contact with vapours. Both from their structure and the results of experiments he concludes that they are olfactory in function and terms them olfactory pores. McIndoo's interpretation of their structure is not supported by the results of other investigators (vide Newton, *Quart. Journ. Mic. Sci.* 1931) and their true sensory function remains problematical.

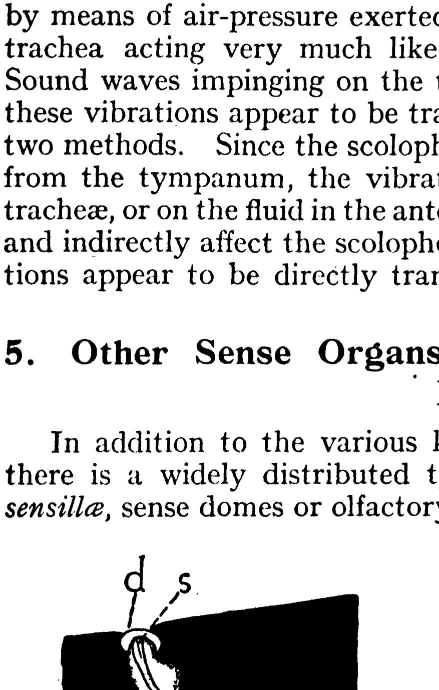

FIG. 101.—CAMPANIFORM SENSILLA FROM THE CERCUS OF *BLATTA ORIENTALIS*.

c, Trichogenous cell; *d*, dome-like covering; *h*, hypodermis; *n*, neurilemma; *nv*, nerve fibre; *s*, scolopala; *sc*, sense cell; *v*, vacuole; (integument deep black). From Sihler.

The halteres of Diptera are richly endowed with groups of sensillæ and are regarded by some investigators as static organs which enable those insects to co-ordinate their movements during flight. Much difference of opinion exists, however, and other observers ascribe to them a chordotonal function.

The elaborate structure known as Graber's organ, found in Tabanid larvæ, is evidently adapted to receive sensory impressions of some kind, but its function is wholly problematical.

In the winged forms of *Phylloxera* Stauffacher (1903) has described what appears to be a true *static organ,* which is located at the base of each fore-wing, between the pro- and meso-thorax. It consists of a small vesicle, enclosing a central body or statolith, together with nervous connections.

Among other sense organs are the *postantennal organs* of Collembola, and the *pseudocelli* distributed over various parts of the body in certain of the latter insects and in the Protura. Nothing definite is known concerning their functions.

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[1] Vide also *Smiths. Misc. Coll.*, 63, 65, 1914, 1916; *Biol. Bull.* 28, 1915; *Journ. Comp. Neur.*, 29, 31, 1917, 1920; *Journ. Morph.* 31, 1918; *Ann. Ent. Soc. Am.* 12, 1919.

THE SOUND- AND LIGHT-PRODUCING ORGANS

IN addition to the organs of special sense there are certain other organs of relation that are very different in character since they are adapted for the production and not for the reception of stimuli. These are the sound- and light-producing organs.

M.Sc. O.U 1967

The Sound-Producing Organs

No insect possesses a true voice but sounds of different kinds and intensity are produced by a number of species scattered through all the great groups. In many cases the property of sound-production is confined to the males: the females, however, are not invariably dumb and some possess the same faculty but in a lesser degree. On the other hand, sexual differences of this kind are frequently wanting and the sound-producing organs exhibit no appreciable differences in the two sexes. The significance of the sounds that are produced is not always easy to infer and, in some cases, it does not appear to be subject to any teleological explanation. In many insects they are undoubtedly concerned with the attraction of the sexes for mating, and in others they serve to communicate some kind of intelligence such as recognition, danger, etc., to other members of a species.

The methods by which sounds are produced may be classified under the following headings.

(*a*) By the tapping of some part of the body against an external object.
(*b*) By the friction of one part of the body against another part.
(*c*) By the vibration of the wings.
(*d*) By the vibration of a special membrane exerted by muscular action.
(*e*) By vibrations of uncertain origin.

A. SOUNDS PRODUCED BY THE TAPPING OF SOME PART OF THE BODY AGAINST AN EXTERNAL OBJECT

The best known example of sounds produced by this method is afforded by beetles of the family Ptinidæ, more particularly those of the genus *Anobium*. The latter insects burrow into old furniture and woodwork where they make ticking or tapping sounds that are believed to be of the nature of a sex call. The sound is produced by an insect striking the lower part of the front of the head against the surface upon which it is resting. The soldiers of some termites (*Termes* spp.) similarly exhibit the habit of striking the floor of their habitation by means of the head, thereby producing a clearly audible sound. In the highest stage of its development a large number of the soldiers may hammer in rhythmic unison. There appears every reason to believe that this practice is a warning signal serving to communicate the existence of danger to other members of the community.

B. SOUNDS PRODUCED BY THE FRICTION OF ONE PART OF THE BODY AGAINST ANOTHER PART

By far the greater number and variety of the sounds emitted by insects are produced by this method, the actual parts concerned with the sound production being known as stridulating organs. Practically every external part of the body which is subjected to friction on an adjoining part has given rise to a stridulating organ in one or other insect.

Stridulating organs are possessed by representatives of several orders of insects, particularly the Orthoptera, Coleoptera, and Hemiptera, but it is in the first mentioned order that they are best known. In many species of the families Acridiidæ, Tettigoniidæ, and Gryllidæ the males are capable of vigorous stridulation: outside these three families very few other Orthoptera stridulate and the faculty is rarely present in the females. Among the Acridiidæ (vide p. 246) the sounds are produced by one of two methods. Either the upper surface of the costal margin of the hind-wing works against the lower surface of the fore-wing or, more usually, the inner aspect of each femur bears a series of pegs which are worked against the outer surface of the corresponding fore-wing (Fig. 102). In the Tettigoniidæ and Gryllidæ (vide pp. 248 and 249) the sound is produced by friction between two modified areas of the fore-wings.

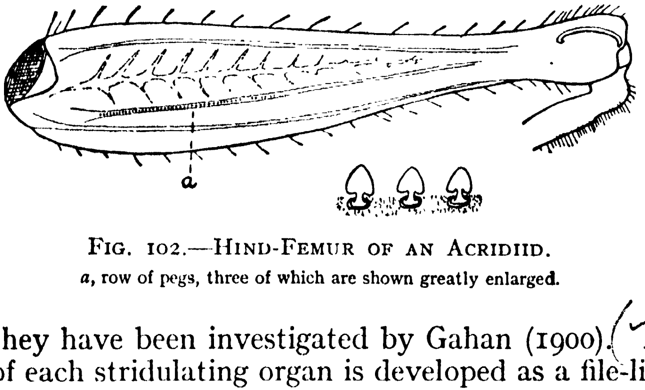

FIG. 102.—HIND-FEMUR OF AN ACRIDIID.
a, row of pegs, three of which are shown greatly enlarged.

Among Coleoptera there is a great variety of stridulating organs which, so far as they were known at the time, were very fully discussed by Darwin in the "Descent of Man"; more recently they have been investigated by Gahan (1900). As a general rule one part of each stridulating organ is developed as a file-like area and the other as a scraper consisting of a point or a series of points which is rasped across it. These organs are generally present in both sexes and equally developed in each, probably serving for mutual sexual calling. The Bostrichid genus *Phanopate* is exceptional among insects in that the stridulating apparatus is confined to the female. In *Heliopathes* on the other hand the female is devoid of stridulating organs, and in species of *Oryctes* the striæ are coarser and more regular in the male than in the female. The remarks of Darwin on stridulation in Coleoptera may be quoted verbatim. "In the case of the Heliopathes and Oryctes there can hardly be a doubt that the males stridulate in order to call or to excite the females; but with most beetles the stridulation apparently serves both sexes as a mutual call. Beetles stridulate under various emotions, in the same manner as birds use their voices for many purposes besides singing to their mates. The great Chiasognathus stridulates in anger or defiance; many species do the same from distress or fear, if held so that they cannot escape; by striking the hollow stems of trees in the Canary Islands, Messrs. Woolaston and Crotch were able to discover the presence of beetles belonging to the genus Acalles by their stridulation. Lastly, the male Ateuchus stridulates to encourage the female in her work and from distress when she is removed."

The larvæ of certain of the Lamellicornia (vide Schiödte 1861–81) are endowed with stridulating organs on the legs or on the mouth-parts: they live in concealed situations and the significance of their sound-producing apparatus has never been adequately explained.

Among Hemiptera there is similarly a great diversity of stridulating organs, more particularly in the Heteroptera. Both sexes frequently possess the power of sound production, but in *Corixa* the mechanism is less perfectly developed in the female. With the exception of certain leaf-hoppers organs of this kind are generally wanting among Homoptera.

Several Lepidoptera are known to be capable of stridulation. According to Hampson (1892) in certain Agaristidæ the male has a corrugated area beneath the costa of the fore-wing, and the wing-membrane is dilated in that region apparently to act as a resonator. It is suggested that the clicking sound which is emitted is produced by the ridged areas on the fore-wings passing over spines on the tarsi during flight. Certain species of *Angeronia* (both sexes) have long been known to make a similar clicking sound, and Hampson has described a stridulating apparatus at the base of the fore-wing. The same author (*Proc. Ent. Soc.* 1894, p. xiii) mentions that the males of *Cidaria dotata* and other species possess a row of spines on a specialized area of the fore-wing which would presumably work against the costa of the hind-wing. A slight rustling, or hissing noise is produced by several of the common European species of *Vanessa* (Swinton, *Ent. Month. Mag.* 1877: *Ins. Life* 1) and a more audible "squeaking" sound by *Halias prasinana* (Swinton, 1877). For sound production in *Acherontia* vide Lepidoptera.)

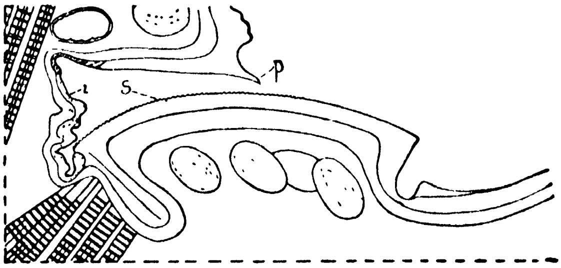

FIG. 103.—STRIDULATING ORGAN OF *MYRMICA LÆVINODIS* IN MEDIAN SECTION.

p, edge of post-petiole forming a "scraper"; *s*, stridulatory surface on first gastric segment; *i*, intersegmental membrane. *After* Janet.

In the Hymenoptera stridulating organs are common among certain ants and vary in structure in different species, and in the castes of the same species (Fig. 103). The organ consists of a file and scraper on the mid-dorsal region of the integument, at the base of the first gastric segment where the preceding segment overlaps. In *Mutilla europæa* both sexes have the power of stridulation, and the organ is very similar in its position and structure to that found in ants.

C. SOUNDS PRODUCED BY THE VIBRATION OF THE WINGS

Certain insects make a humming or buzzing sound when flying which is brought about by the vibration of the wings. Sounds of this description are particularly audible in such large insects as *Melolontha*, *Geotrupes* and *Bombus*. They are not, however, to be confused with other and higher pitched sounds, which may be made at the same time by a different method. Lubbock mentions that from the note produced the rapidity of the vibration can be calculated. Thus, the house-fly, which produces the sound of F, vibrates its wings 335 times a second, and in the bee, which makes a sound of A, the vibrations are at the rate of 440 in a second. Marey has succeeded in confirming these numbers graphically by fixing an insect so that the extremity of the wing just touched a revolving cylinder. Each stroke of the wing caused a perceptible mark and he thus showed that a house-fly for example, made 330 strokes in a second which agrees very closely with the number inferred from the note produced. (Bellesme, however, concludes that sounds corresponding to vibrations of this frequency are produced by extremely rapid changes in the contour of the thorax and are maintained after removal of the wings (vide also p. 103). By attaching a style to the tergal part of the thorax he obtained a record of these vibrations which corresponded in frequency to those required to produce the sound that was experienced.

D. SOUNDS PRODUCED BY THE VIBRATION OF A SPECIAL MEMBRANE EXERTED BY MUSCULAR ACTION

Among the Cicadidæ there is found one of the most complex kinds of sound-producing organs known. These structures are met with in the males, the females being either silent or only possessing rudiments of the apparatus. (The great volume of sound emitted by the cicadas marks them out as being the noisiest representatives of the Insecta.

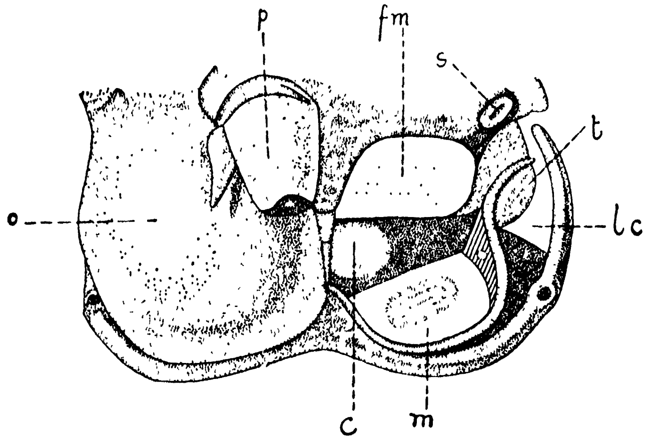

FIG. 104.—SOUND-PRODUCING APPARATUS OF A CICADA WITH THE OPERCULUM OF ONE SIDE REMOVED.

c, ventral cavity ; *fm*, folded membrane ; *lc*, lateral cavity ; *m*, tympanal organ ; *o*, operculum, that of the other side removed ; *p*, base of leg ; *s*, spiracle ; *t*, timbal. *After* Carlet, *Ann. Sci. Nat.* 1887.

The apparatus, and the sounds produced by it, have been studied by many observers, but the basis of our knowledge of the structure and mode of working of the mechanism will be found in the very full and accurate description of Reaumur (*Hist. des Ins.* V. 1740). His observations were confirmed and extended by Solier and later by Carlet (1887).

(The organs in question comprise a pair of shell-like drums or timbals situated at the base of the abdomen. These drums vibrate by the action of powerful muscles, and the sound can be variously modified by the so-called mirrors or sounding boards. In *Cicada septendecim* the true sound organs are freely exposed, but in many other cicadas the drums are covered by overlapping plates or opercula.)

In the more perfect form of the apparatus, which is exhibited for example in *Cicada plebeia*, the account given by Carlet may be followed (Fig. 104). In this species the *opercula* are a pair of large plates which are backward extensions of the metasternellum, and situated on the ventral side of the body, where they overlap the base of the abdomen. On removing an operculum a pair of cavities containing the external parts of the sound-producing apparatus is disclosed. The larger of these cavities is ventral, and the smaller is lateral in position. Their walls contain three specialized areas of membrane which are known respectively as the ***timbal***, the ***folded membrane*** and the ***mirror***. The ***timbal*** is a crisp, plaited membrane surrounded by a chitinous ring ; it forms part of the inner wall of the lateral cavity, and is somewhat shell-like in appearance with its convex surface bulging outwards. The folded membrane is in the anterior wall of the ventral cavity, while the mirror is a tense, mica-like membrane in the posterior wall of that cavity. In close association with the whole apparatus there is an extensive air-chamber which opens to the exterior by means of the third pair of spiracles. The sound is produced by the rapid in and out movement of the timbal, which is brought about by a powerful muscle. The latter arises from the mesofurca and is attached to the inner face of the timbal. When the muscle contracts the timbal is pulled inwards: on the relaxation of the muscle the timbal regains its former position in virtue of the elasticity of its chitinous ring. This method of sound production has been compared to the pushing in and out of the bottom of a tin vessel, which makes a cracking sound. The destruction of the timbal of both sides of the body renders the insect silent. The sound can also be modified by the operculum which is capable of being slightly elevated, but its main function is protective. The so-called mirror is a true tympanal organ which appears to be capable of perceiving sound vibrations (vide p. 94) and plays no part in sound production.

E. SOUNDS PRODUCED BY VIBRATIONS OF UNCERTAIN ORIGIN

In certain insects, particularly Diptera, sounds are produced in a manner different from those already referred to. The actual method of sound production in these cases has given rise to much discussion, and the evidence that is available is of a conflicting nature. Many entomologists are familiar with the highly pitched singing note that is emitted by various flies, particularly in some species of Syrphidæ, both when hovering and when at rest. Somewhat similar notes are produced by several Coleoptera and by Hymenoptera. According to Landois (1867) the sound is caused by the vibration either of a series of lamellæ, or a tongue-like fold, projecting into the lumen of the trachea close to certain of the spiracles. These structures are membranous infoldings of the tracheal intima which are believed to be set in vibration by the forcible passage of air through the spiracles, thus producing a highly pitched note. Landois states that if the head, wings, legs and abdomen of a *Calliphora* be removed, so that the thorax is left with no vibratory parts other than the halteres, the highly pitched note is maintained. If the thoracic spiracles be closed with gum or wax the sound ceases. Lowne has described peculiar tympanic chambers immediately behind the insertions of the wings in *Calliphora* and in close association with the corresponding spiracles. He concludes that the emission of sounds in this insect is due to the expulsion of air through the thoracic spiracles, and the vibration of a membrane in the tympanic organ. He also mentions that the whole thorax vibrates distinctly when the insect is held between the finger and thumb. Bellesme (*Comp. Rend.* 87, 1878) notes that in Diptera and Hymenoptera the highly pitched sounds continue after removal of the wings and the stoppage of the spiracles. He considers that they are due to very rapid changes in the form of the thorax—in fact a kind of thoracic vibration—due to contractions of the wing muscles. J. Perez (*Comp. Rend.* 87, 1878) from a study of certain Diptera also finds that the sounds continue when the spiracles are artificially closed, and attributes them to vibrations of the wing bases against certain closely associated sclerites. The fact that different observers have not always used the same species of insect in their experiments may explain some of the discrepancies in the results obtained, but the subject is clearly one in need of renewed investigation.

The Light-Producing or Photogenic Organs

Certain insects are self-luminous owing to the possession of special photogenic organs: some other insects owe their luminous properties to the presence of light-producing bacteria, or on account of having ingested luminous food.

True luminous insects are almost confined to the order Coleoptera and more particularly to various genera of Cantharidæ (Lampyrinæ), notably *Lampyris, Luciola, Phosphænus, Photurus, Photinus, Phengodes* and others. The Elaterid genera *Pyrophorus* (the "cucujos") and *Photophorus* are also luminous, and the same remark applies to several species of the Carabid *Physodera* and to *Buprestis ocellata*. Outside the Coleoptera, the larva of the Mycetophilid *Bolitophila luminosa* has photogenic powers. A small number of other insects are also luminous but are not known to possess special organs for the purpose, and in many cases the light is probably associated with the presence of bacteria. Examples of this kind include *Lipura noctiluca*, a few Ephemeroptera, together with certain larval Diptera and Lepidoptera.

In the Cantharidæ, previously mentioned, the luminosity is known in some species to extend to all the developmental stages, and is a character of their plasma. In the egg the luminous substance is diffused, but in the post-embryonic phases it is localized in the photogenic organs. The latter are usually situated on the ventral aspect near the apex of the abdomen, except in *Phengodes* where they are distributed along the sides of the body. In *Lampyris noctiluca* the female is apterous and larviform (and also in *Phengodes*) yielding a bright light, while the male is winged and has a feebler photogenic capacity. In *Lucioli italica* both sexes are winged and luminous and the same condition is found in the Elateridæ. In the latter the chief photogenic organs are situated on the dorsal aspect of the thorax. It is generally believed that the light in the above instances serves to ensure the meeting of the sexes, but its significance in the earlier stages is not understood.

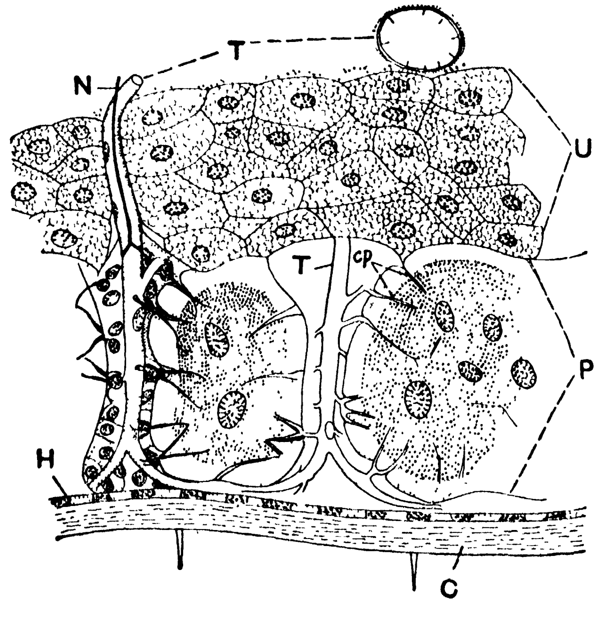

FIG. 105.—LUMINOUS ORGAN OF PHOTINUS.

C, cuticle; *cp*, tracheal capillaries; *H*, hypodermis; *N*, nerve; *P*, photogen layer; *T*, tracheæ; *U*, reflector layer. *After* Williams, 1916.

The luminous organs, in all stages of the species concerned, exhibit the same essential structure. They consist of an outer or photogen layer and an inner or reflector layer (Fig. 105). Tracheæ and nerves penetrate both layers but are more highly developed in the outer stratum. Each organ is covered by the general cuticle of the body which is more translucent than elsewhere. The *photogen layer* is transparent and its cells are grouped into lobules which are associated with the larger tracheal branches ; the smaller vessels from the latter terminate in end-cells with tracheoles. The exact distribution of the tracheæ varies in different species, but in all cases the arrangement is such as to provide a very abundant oxygen supply. The *reflector layer* is composed of cells containing numerous urate crystals ; they have a milky appearance and act as a background scattering the incident light and preventing its dispersal internally.

Much discussion has taken place with regard to the morphological origin of the photogenic organs. Dubois and others maintain that they are derived from the hypodermis, but Vogel and Williams, who have both studied the development of these organs, state that they are derived from the fat-body. In the larva of *Bolitophila* they are exceptional in being formed from modified portions of the Malpighian tubes.

The phenomenon of light-production in the animal and vegetable kingdoms is one of luminescence, the light emission being stimulated by some means other than heat. The term phosphorescent organs has often been applied to the luminous organs of insects and other animals, but the light produced is in no sense a phosphorescence since it is independent of the previous illumination of the organism. The light is emitted as the result of the oxidation of a compound *luciferin* in the presence of an enzyme-like substance *luciferase*. This reaction takes place within the cells of the luminous organ and is dependent upon oxygen and water for its consummation. The amount of heat generated during the reaction has been studied by Harvey who prepared luciferin and luciferase extracts from the Ostracod *Cypridina*. As the result of his experiments he found that if any rise of temperature occurs during the luminescence, which results from the mixing of these two substances, it is certainly less than ·001° C. ; or, 1 gram luciferin liberates less than 10 calories during the luminescence accompanying oxidation. The physical nature of animal light is not in any way different from light of ordinary sources except in intensity and spectral effect. It is visible light containing no infra-red or ultra-violet radiation, or rays which are capable of penetrating opaque objects. It is not polarized as produced but is polarizable by a Nichol prism : it will cause fluorescence and phosphorescence of substances and affect a photographic plate (vide Harvey, 1920).

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THE DIGESTIVE SYSTEM AND ITS APPENDAGES

THE alimentary canal is a tube of very variable length ; in some cases it is about equal to that of the body, while in others its length is greatly increased and it assumes a convoluted course. The shortest and simplest type is found in many larvæ, notably those of the Lepidoptera, Hymenoptera, and Diptera-Nematocera ; in the Apterygota, Dermaptera, certain Orthoptera, etc., this condition is maintained throughout life. In nymphal and adult Homoptera, and in the larval Diptera Cyclorrhapha, it attains its greatest length and number of convolutions and is often several times longer than the whole insect. As a general rule, it may be said that the greatest length of digestive canal is to be found in those insects which feed upon juices, rather than upon the more solid tissues of animals and plants. Exceptions, however, are found in the larval Hymenoptera, whose aliment is entirely of a fluid nature, and whose digestive canal is a straight, simple tube. Morphologically the alimentary canal is divisible into three primary regions according to their method of embryonic origin (Fig. 106). The *fore-intestine* arises as an anterior ectodermal invagination (stomodæum) : the *hind-intestine* as a similar posterior invagination (proctodæum) ; and the *mid-intestine*, which ultimately connects the two, develops as an endodermal sac (mesenteron). These differences in embryonic origin result in marked histological differences in the structure of the mid-intestine, as compared with either of the other regions. Both the fore- and hind-intestine, being invaginations of the body-wall, resemble the latter in their essential histology, and are lined with chitin.

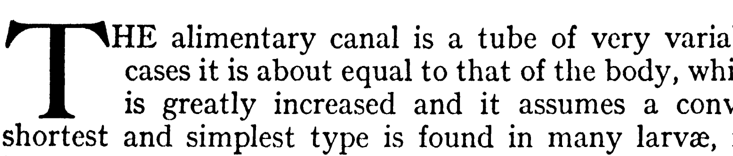

FIG. 106.—DIAGRAM OF THE DIGESTIVE SYSTEM OF AN INSECT.

The ectodermal parts are represented by heavy lines and the endodermal parts by broken lines.

m, mouth ; *oe*, œsophagus ; *c*, crop ; *g*, gizzard ; *ec*, enteric cœca ; *mg*, mid-intestine ; *mt*, Malpighian tubes ; *ht*, hind-intestine ; *r*, rectum ; *a*, anus.

(*a*) The Fore-Intestine

The following layers, passing from within outwards, are generally recognizable in the walls of the fore-intestine (Fig. 107 A). 1. The ***intima*** or innermost lining, which takes the form of a chitinous layer directly continuous with the cuticle of the body-wall. 2. The ***epithelial layer*** continuous with the hypodermis and, like the latter, chitogenous in function : it is often extremely thin and may take the form of a syncytium. 3. The ***basement membrane*** bounding the outer surface of the epithelium. 4. The ***longitudinal muscles.*** 5. The ***circular muscles.*** 6. The ***peritoneal*** *membrane* which consists of apparently structureless connective tissue and is often difficult to detect. The fore-intestine is divisible into the following regions :—

The *pharynx*. The term pharynx is given to the region immediately behind the mouth, between the latter opening and the œsophagus. In biting insects the mouth is bounded by the labrum above, the labium below and by the mandibles and maxillæ on either side. In sucking insects a true mouth is absent, the actual entrance into the digestive system being situated at the apex of the organ of suction. The pharynx is best developed in the latter type of insects, and is provided with an elaborate musculature, many of whose fibres pass outwards to be attached to the wall of the head. By means of these muscles it functions as a pumping organ, which serves to imbibe the liquid food through the proboscis and convey it backward into the œsophagus.

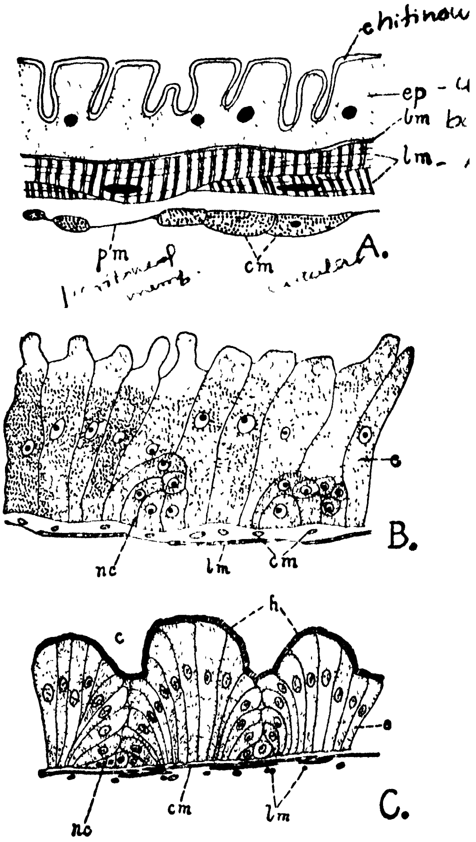

FIG 107.—A. LONGITUDINAL SECTION OF THE WALL OF THE ŒSOPHAGUS OF A TERMITE.

c, chitinous intima ; *ep*, cellular layer ; *bm*, basement membrane ; *lm*, longitudinal muscles ; *cm*, circular do., *pm*, peritoneal membrane.

B. LONGITUDINAL SECTION OF THE WALL OF THE MID-INTESTINE OF A TERMITE IN THE SECRETORY PHASE.

e, enteric epithelium ; *nc*, group of regenerative cells; other lettering as in A.

C. TRANSVERSE SECTION OF THE WALL OF THE MID-INTESTINE OF *BLATTA* IN THE RESTING PHASE.

c, crypt ; *h*, striated hem.

The *œsophagus* is a simple, straight tube passing from the hinder region of the head into the fore part of the thorax. It is very variable in length and the inner walls are longitudinally folded.

The *crop* is present in many insects and is a dilatation of the hinder portion of the œsophagus. It is extremely variable in form, and functions as a food reservoir ; its walls are thin and the muscular coat weakly developed. In *Periplaneta*, and most Orthoptera (Fig. 109), it is very capacious and constitutes the major portion of the fore-intestine. In a few insects it is developed as a lateral dilatation of one side of the œsophagus as in *Gryllotalpa*, certain of Isoptera and the larvæ of *Myrmeleon* and the Curculionidæ. Among various sucking insects this dilatation becomes greatly pronounced and connected with the œsophagus by means of a slender tube. The organ is then known as the food-reservoir or "sucking stomach," but the latter expression is misleading and incorrect. A food-reservoir is present in most Diptera (Fig. 109) and also in the larvæ of some of the Cyclorrhapha and in the higher Lepidoptera (Fig. 110).

The *proventriculus* or *gizzard* (Fig. 111) is situated behind the crop and is principally developed in mandibulate insects which feed upon hard substances ; among the Orthoptera it is a very highly specialized organ

(Fig. 108). It is also found in many carnivorous and wood-boring Coleoptera, the Mecoptera, Odonata, Isoptera and various Hymenoptera; it is reduced to the condition of a valve in the honey bee and most of the Diptera. The dominant feature in its structure is the great development of the chitinous lining into prominent denticles, and the increased thickness of its muscles. At the point of junction of the fore- and mid-intestine, there is present in many insects a *cardiac* or *œsophageal valve.* This structure is formed by the wall of the fore-intestine being prolonged into the cavity of the stomach as an inner tube, which then becomes reflected upon itself and passes forwards to unite with the stómach-wall (Fig. 112). It exhibits varying degrees of complexity among different insects and, in certain Dipterous larvæ, a blood sinus is present between its outer and inner walls (Imms, *Journ. Hyg.* 1907, p. 301).

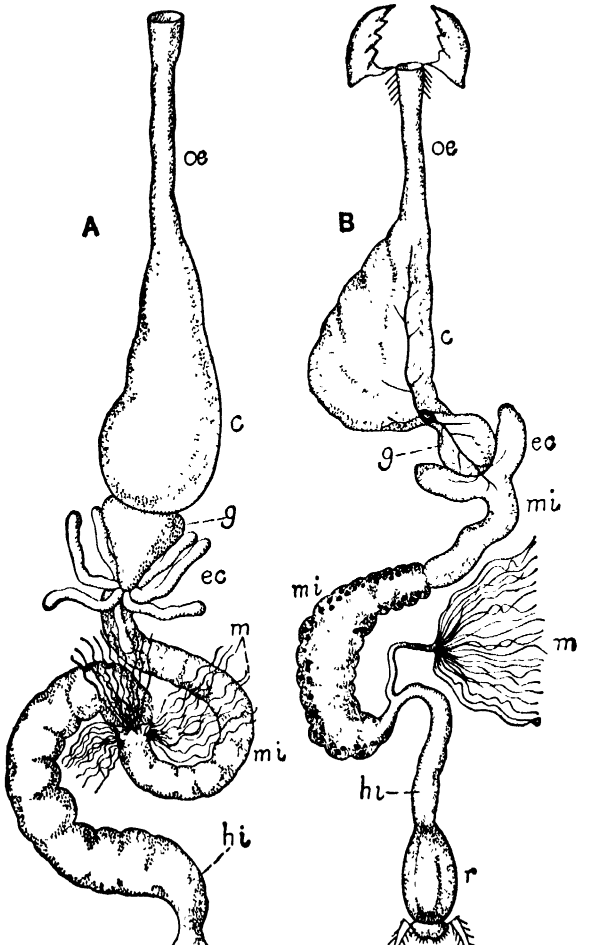

FIG. 108.—A. ALIMENTARY CANAL OF *PERIPLANETA AMERICANA.* B. ALIMENTARY CANAL OF *NEMOBIUS SYLVESTRIS* (GRYLLIDÆ).

oe, œsophagus; *c*, crop; *g*, gizzard; *ec*, enteric cœca; *m*, Malpighian tubes; *mi*, mid-intestine; *hi*, hind-intestine; *r*, rectum; *rp*, rectal papillæ. *After* Bordas, *Ann. Sci. Nat.*, 8*th ser.*, 5.

(*b*) The Mid-Intestine

This region is termed the *stomach* or *mid-gut* and its shape and capacity vary exceedingly. In some cases it is sac-like, in others it is coiled and tubular like an intestine, or it may be divided into two well-defined regions as in many Cyclorrhapha (Fig. 109). Histologically the wall of the stomach exhibits the following structure (Fig. 107). Internally it is lined by a stratum of ***enteric epithelium*** the outer ends of whose cells rest upon a ***basement membrane***: the latter is followed by an inner layer of ***circular muscles*** and an outer layer of ***longitudinal muscles.*** The outermost coat of the stomach is thin ***peritoneal membrane.*** Both muscle layers are composed of striated fibres and their positions are the reverse to what obtains in the fore-intestine. The structure of the enteric epithelium requires more detailed mention. Its cells are usually clearly demarcated and during the non-secretory phase their inner or free margin is bounded by the so-called *striated hem*. The appearance of the latter, in many cases, appears to be due to minute pore canals while in others closely set cilia-like processes are described (vide Vignon, 1901). In the active or secretory phase the cells give off granular protrusions, which extend into the lumen of the stomach, where they either become disconnected or rupture, thereby discharging their secretory contents. The epithelial layer is generally folded to a greater or lesser degree, and beneath the crypts of the folds, or between the epithelial cells, are islands of small cells which are centres of regeneration replacing those which are no longer functional. As a general rule the enteric epithelium exhibits no special differentiation of its cells in conformity with the dual function of secretion and absorption, each cell being capable of performing both acts during its physiological phases (Steudel,

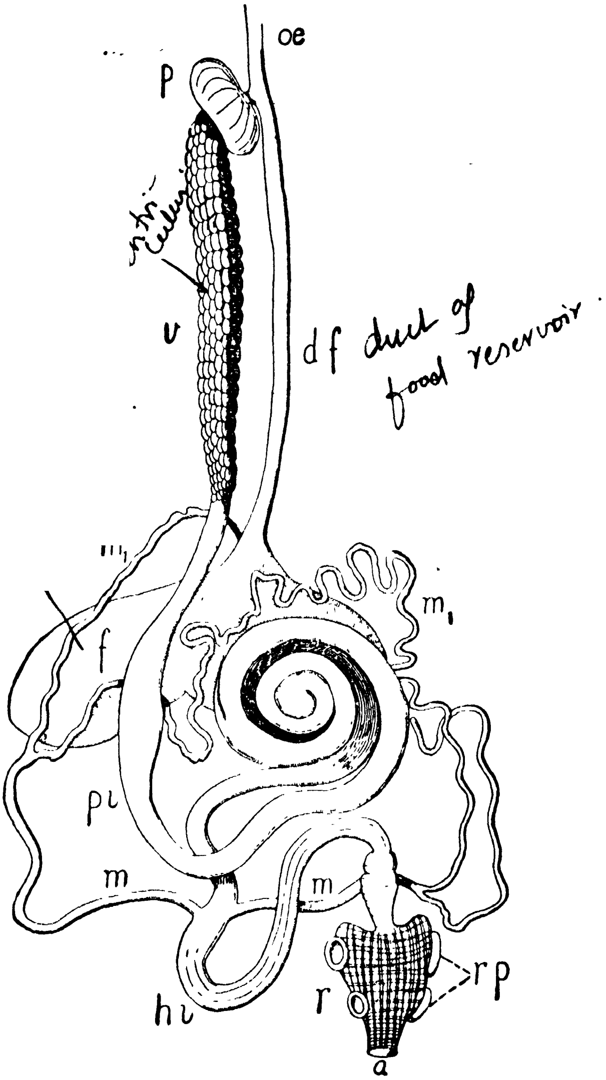

FIG. 109.—ALIMENTARY CANAL OF A MUSCID FLY (CALLIPHORA).

oe, œsophagus; ***p***, proventriculus; ***v***, ventriculus; ***df***, duct of food-reservoir ***f***; ***p i***, proximal intestine; ***m_1***, Malpighian tubes which unite to form a common stem (***m***) on either side; ***hi***, hind intestine; ***r***, rectum; ***rp***, rectal papillæ; ***a***, anus. Adapted from Lowne.

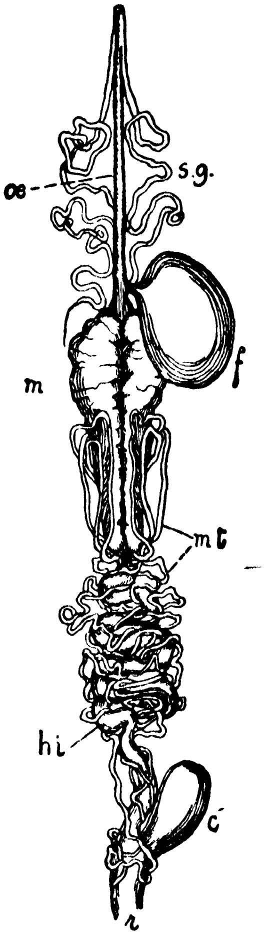

FIG. 110.—DIGESTIVE SYSTEM OF *SPHINX LIGUSTRI* (IMAGO).

œ, œsophagus; ***s g***, salivary gland; ***f***, food-reservoir; ***m***, mid-intestine; ***m.t***, Malpighian tubes; ***hi***, hind intestine; ***c***, cœcum; ***r***, rectum. *After* Newport.

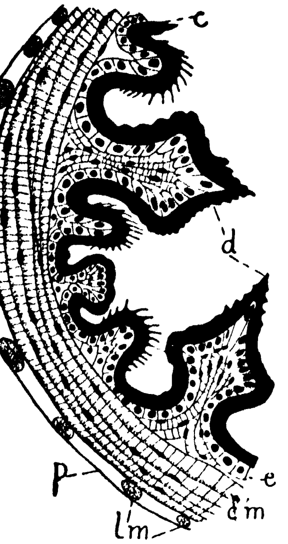

FIG. 111.—TRANSVERSE SECTION OF THE WALL OF THE GIZZARD OF LOCUSTID (*DETICUS ALBIFRONS*.

c, chitinous lining; *d*, teeth; *e*, epithelium; *cm*, circular muscles; *lm*, longitudinal muscles; *p*, peritoneal membrane. *After* Bordas.

1913). In a few insects, however, notably in *Ptychoptera*, van Gehuchten (1890) states that the absorptive cells are very large and located in a definite region between two areas occupied by secretory cells. It is frequently found that the stomach is lined by a membranous tube which, for the most part, is not in contact with its epithelium (Fig. 112). This tube is the *peritrophic membrane* of Balbiani; it is quite colourless and, on account of its resistance to the action of alkalies, it is inferred to be of a chitinous nature. The seat of its origin is a band of deeply staining gland cells situated at the junction of the fore- and mid-intestine (vide Gehuchten 1890, Vignon 1901, Wigglesworth 1930 and others). Its first appearance is as a fluid in the space between the glandular zone and the reflected wall of the fore-intestine. According to Wigglesworth, compression of the cardia results in the secretion being drawn through a kind of annular press so as to become moulded into a membranous tube which gradually passes backwards during its formation. Functionally, the peritrophic membrane seems to protect the mid-gut epithelium from abrasion and it is generally absent in insects which feed upon fluid diet. The apparent absence of mucous cells from the epithelial layer is possibly correlated with the development of the peritrophic membrane.

A membranous tube surrounding the ingested food is present in the Thysanura, Orthoptera, many Neuroptera and Coleoptera, certain Hymenoptera, in larval Lepidoptera and many larval Diptera. On the other hand, Schneider states that it is wanting in the Hemiptera, adult Lepidoptera, many carnivorous Coleoptera and in many Hymenoptera.

In the hive-bee (Snodgrass), the larva of *Æschna* (Voinov) and certain other insects a peritrophic membrane is described as being formed by the delamination of the inner or free margin of the cells lining the mid-intestine. It is evident that in these instances it is a non-chitinized structure quite different from the usual type of peritrophic membrane described above.

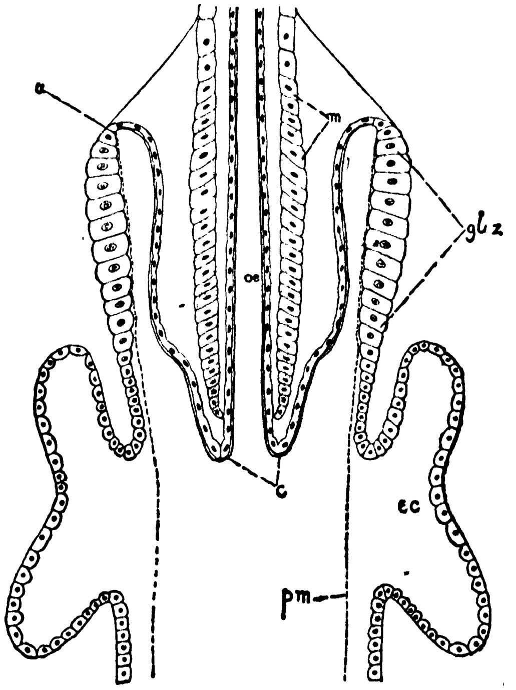

FIG. 112.—CARDIA OF A DIPTEROUS LARVA (NEMATOCERA) WITH THE ADJACENT REGION OF THE MID-INTESTINE, SEEN IN LONGITUDINAL SECTION.

oe, œsophagus; *c*, chitinous intima; *m*, muscles; *u*, point of union of fore-intestine with mid-intestine; *glz*, zone of columnar gland cells which secrete the peritrophic membrane *pm*; *ec*, enteric cœcum.

In many insects the surface area of the stomach is increased by the development of sac-like diverticula,—the *enteric* or *gastric cœca* (Fig. 108).

These organs are usually situated at the œsophageal end of the stomach and are very variable in number. In certain dipterous larvæ and in the Gryllidæ and Locustidæ two large cœca are present; in *Periplaneta* and larval Culicidæ there are eight, while in the larva of *Oryctes nasicornis* they are more numerous and are disposed in an anterior, a median, and a posterior annular series. Among various predaceous Coleoptera they are represented by numerous villiform processes, and in some orders (e.g. Collembola, Lepidoptera) cœca are generally wanting.

In the larvæ of certain groups of insects the stomach is a closed sac, the passage being closed between the mid- and hind-intestine. In these instances the food is always of a fluid nature and there is but little solid residuum. This condition is prevalent in the majority of the larvæ of the Hymenoptera Apocrita, and in those of the Neuroptera Plannipennia, of *Glossina*, and other viviparous Diptera.

(*c*) The Hind-Intestine

This region consists of the same layers as the fore-intestine except that its circular muscles are developed to a varying degree both inside and outside the layer of longitudinal muscles. The commencement of the hind-intestine is marked by the insertion of the Malpighian tubes (vide p. 140) which are likewise of ectodermal origin. In most insects three well marked regions are recognizable. These are:—the *small intestine* or *ileum*, the large intestine or *colon* and the *rectum*. The chitinous lining of the ileum and colon is often thrown into folds and provided with hair-like or spinous projections: among certain Lamellicorn larvæ the latter are highly developed and assume an arborescent form. The ileum may be very long as in *Dytiscus* and *Necrophorus*, short as in many other insects, or it may be undifferentiated from the colon, as in many Orthoptera and Hemiptera. Among Lepidoptera, certain Coleoptera, etc., a hollow outgrowth or cœcum arises from the colon: it is sac-like in *Sphinx ligustri* (Fig. 110) and many other Lepidoptera, while in *Dytiscus* it takes the form of a tube nearly equal to the abdomen in length. The *rectum* is a more or less globular or pyriform chamber, generally provided with a variable number of inwardly projecting papillæ or "rectal glands." The latter are six in number in Orthoptera and Neuroptera, very numerous in Lepidoptera but are absent in many insects, particularly in their larvæ. They are composed of specially large cells, well supplied with tracheæ, and bounded by cuticle. The functions of the rectal papillæ have been much discussed, many authorities regarding them to be glandular organs. Recent observations by Wigglesworth (1932) lend support to the view that these papillæ, or the general rectal epithelium in their absence, are concerned with the reabsorption of water from the excrement before the latter is voided and, in this way, it is claimed, the water content of the insect is conserved.

(*d*) Physiology of the Digestive System

The chemistry of digestion in insects has an extensive literature (Uvarov, 1929), but detailed studies of the processes involved are few. The subject has been most fully investigated in cockroaches whose digestive processes are but little specialized and a full complement of enzymes are present (vide Swingle 1925, Wigglesworth 1927–28 and others). The food, upon entering the buccal cavity, is subjected to the action of amylase produced by the salivary glands which convert starch into maltose. The secretion of the mid-intestine and the enteric cœca resembles that of man except for the absence of pepsin and hydrochloric acid. In so far as carbohydrate digestion is concerned, maltase, invertase and lactase are involved, while a trypsin and an erepsin are concerned with the digestion of proteins, and fats are dealt with by a lipase. The solid food is held back by the gizzard which acts as a strainer, only admitting fluid matter into the mid-intestine. The secretion of the latter region passes forwards into the crop where the major part of the digestion probably occurs. The contents of the mid-intestine have a *p*H of 6·2 but in the crop an acid reaction is evident with an average *p*H of 5·2, varying according to the nature of the food. The acidity results, according to Wigglesworth, from the action of microörganisms upon the carbohydrates present. Among blood-sucking insects an anti-coagulin is commonly produced by the salivary glands and in *Glossina*, which is adapted to a diet of blood, the mid-intestine contains abundant trypsin and erepsin but, apart from a weak amylase, carbohydrate-splitting enzymes are wanting. Wigglesworth (1929) has contrasted this condition with that obtaining in *Calliphora* whose salivary glands produce an active amylase. In the mid-gut amylase, invertase and maltase are abundant, whereas proteolytic enzymes are weak.

Among Lepidoptera the digestive enzymes of the oriental peach moth (*Laspeyresia molesta*) have been investigated by Swingle (1928). In the larva invertase, lipase, trypsin and erepsin are present in the mid-intestine, digestion taking place under slightly alkaline conditions. In the adult the only enzyme that could be detected is invertase, a fact which suggests that cane sugar is the principal food and is derived from nectar.

Specialized types of digestion.—Many insects feed on woody tissues and even on dead wood, but very little is known as to whether they are able to digest cellulose. It is generally considered that where such digestion occurs it is by the intervention of symbiotic microörganisms. The problem has been most fully studied in wood-feeding termites which harbour immense numbers of symbiotic Protozoa in the intestinal tract. Wood consumed by the termites is ingested by the Protozoa which utilize the cellulose constituent. Cleveland (1924–28) has shown that by subjecting the termites to a temperature of 36° C. the Protozoa are killed and a similar result was obtained by increasing the oxygen tension of the air by 3 to 4 atmospheres. Termites thus defaunated die, and if given a diet of wood are unable to digest it in the absence of Protozoa. On the other hand, they were able to live for a long period, and perhaps indefinitely, upon humus or fungus-digested cellulose. If the Protozoa be re-introduced the termites regain their ability to live on a diet of wood. Cleveland has also shown that termites are able to live and reproduce on nitrogen-free cellulose so long as Protozoa are present. Since the latter organisms multiply and die in thousands within their hosts their remains would seem to provide the nitrogen required. Other types of wood-feeding insects have been studied by Buchner (1928; 1930) from the anatomical standpoint, and most of them were found to harbour various microörganisms in special chambers or diverticula of the gut. These relations suggest that such organisms are symbionts concerned with cellulose digestion, but there is at present very little proof of the contention. Werner (*Zeits. Morph. Okol. Tiere*, 1926, 6) has shown that in larvæ of the beetle *Potosia cuprea*, which feed on dead pine needles, cellulose-digesting bacteria are present in special chambers of the intestine. On the other hand, biochemical studies by Ripper (1930) indicate the presence of a cellulase in the digestive juices of some insects devoid of symbionts, while no such enzyme was found in other forms which harbour these microörganisms. Further research is greatly needed to solve this complex problem.

External digestion has been observed in diverse orders of insects; in some cases it is of a preliminary nature only, while in others, the essential processes of digestion appear to take place outside the body. In the Hemiptera the saliva is injected into the tissues of the plant and the enzymes which it contains act upon starch (Bugnion). The larva of *Cossus* discharges a secretion of the mandibular glands which softens the wood upon which it subsequently feeds and thereby admits of its mastication. Fabre (Souv. Ent. 10^e Ser.) states that the larva of *Lucilia cæsar* discharges its digestive secretion over the carrion which serves as its food. By means of a ferment analogous to pepsin the protein matter is liquefied and subsequently imbibed. This explanation, however, is disputed by Guyenot (1907) who states that the digestive secretion exhibits no such properties and that the functions ascribed to it by Fabre are in reality performed by a symbiotic Micrococcus, which is abundant in the food reservoir. Neither Fabre's nor Guyenot's conclusions are supported by those of Hobson (*Journ. Exp. Biol.*, 1931–32) on the nutrition of Blow-fly larvæ (*Lucilia*). Hobson finds that the larvæ imbibe the liquid constituents of their food and that there is no evidence of pre-digestion by means of bacteria. On the other hand, they fail to grow at the usual rate on sterilized meat and it appears that the chief part bacteria play in nutrition is in supplying a growth-promoting substance. In the larvæ of the Dytiscidæ Portier (1911) observes that their jaws pierce the tissues of the prey; the latter is paralysed by the secretion of the glands of the œsophagus which enters through the perforate mandibles. The insect then injects the secretion of the stomach which is rich in zymases, and digestion of the tissues of the prey takes place *in situ*. The *Dytiscus* proceeds to imbibe its prepared meal, afterwards making further injections, the process being repeated until the tissues are consumed. The method of feeding in the larvæ of the Planipennia is very similar, and probably external digestion takes place in these cases also.

Literature on the Digestive System

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THE RESPIRATORY SYSTEM

IN the vast majority of insects respiration takes place by means of internal air-tubes known as *tracheæ*. The latter ramify through the organs of the body and the appendages, the finest branches being termed *tracheoles*. The air enters the tracheæ through paired and usually lateral openings termed *spiracles* (or *stigmata*), which are segmentally arranged along the thorax and abdomen. More rarely the spiracles are closed or wanting, respiration in such cases being cutaneous. In the immature stages of most aquatic insects special respiratory organs known as *gills* (or *branchiæ*) are present, and these may or may not co-exist with open spiracles. The respiratory organs of insects are always derived from the ectoderm: the tracheæ are developed as tubular invaginations of that layer and the gills arise as hollow outgrowths. Histologically, both types of organ are composed of a layer of cuticle, the hypodermis and usually a basement membrane, all of which are directly continuous with similar layers forming the general body-wall.

The Spiracles

Number and Position of the Spiracles.—The spiracles are, morphologically, the mouths of the ectodermal invaginations which give rise to the tracheal system. They are normally placed on the pleura of the thoracic and abdominal segments, but their exact position is very variable. In the abdomen of most insects they are seen to lie in the soft membrane between the terga and sterna. From this position the spiracles may come to be situated either forward or backward in relation to their segments. In many insects, particularly on the thorax, the spiracles assume an intersegmental position, being situated just in front of each of the segments to which they properly belong: or, they may be no longer situated on the pleura but come to lie on the terga, near the side margins of the latter, as is seen in the abdominal spiracles of *Apis* and *Musca*. The whole question of the primitive situation of the spiracles, and the secondary positions assumed by these organs, is one needing investigation.

In the developing embryo the spiracles appear as a series of invaginations lying to the outer side of the rudiments of the appendages. Twelve evident pairs of spiracles are present in the embryo of *Leptinotarsa*, being situated on each of the thoracic and the first nine abdominal segments. In the embryos of most insects, however, the prothoracic pair is wanting and frequently the pair on the 9th abdominal segment is likewise absent. It is noteworthy that although 12 pairs of spiracles are not present in the post-embryonic stages of any one insect, nevertheless, if the spiracle-bearing segments in different orders be taken collectively, they are 12 in number.[1] The maximum number of spiracles recorded in any adult insect is 11 pairs which are present in *Japyx solifugus*: in this species they are located on the first 10 postcephalic segments and there is a supernumerary pair on the metathorax (Fig. 113). According to Silvestri 11 pairs of spiracles are also present in *Evalljapyx.* No other insects, whether they be larvæ or imagines, retain more than 10 pairs of spiracles (2 thoracic and 8 abdominal) which is the prevalent number in the adults of most orders. Among the principal exceptions are the Anoplura which have 1 thoracic and 6 abdominal pairs: the Thysanoptera usually have 1 or 2 pairs of thoracic and 2 pairs of abdominal spiracles; in the Hemiptera Sternorhyncha their number is very variable and is reduced to 2 pairs in many Coccidæ. Among Coleoptera, the Lamellicornia and Rhynchophora have from 1 to 3 of the hindmost abdominal spiracles wanting or non-functional. The Diptera usually exhibit a reduction in the number of abdominal spiracles and, among the Athericera, a sexual difference is evident in this respect, the females often having 5 pairs and the males 6 or 7 pairs. The Lepidoptera usually have 9 pairs of spiracles and many of the Hymenoptera 10 pairs: this number is exhibited, for example, in ants. Among the parasitic Hymenoptera reduction is frequently evident and in the Chalcidoidea, there are commonly only 3 pairs which are situated on the thorax, propodeum and 8th abdominal segment, respectively.

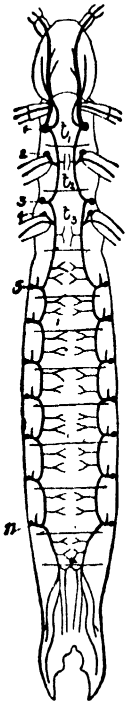

FIG. 113.—TRACHEAL SYSTEM OF *JAPYX.*

t_1, t_2, t_3, thoracic segments; 1–4, thoracic spiracles; 5, 11, abdominal spiracles. *After* Grassi, 1887.

Among adult winged insects there is no indubitable instance of pro-thoracic spiracles being present. Those often regarded as belonging to this segment pertain in all probability to the mesothorax, having undergone a secondary forward migration.

Although functional spiracles are present on the head in the Symphyla, they are not found in that position in any insect. According to Nelson a pair of evanescent spiracles is present on the second maxillary segment in the embryo of the honey bee. Several observers have claimed that from 2 to 5 pairs of cephalic spiracles are represented by the invaginations which give rise to the apodemes forming the tentorium. The balance of evidence, however, is against this homology, since a pair of tentorial invaginations coexist with the spiracles on the second maxillary segment in the embryo bee, and apodemes are present along with spiracles in the thorax of most insects.

Structure of the Spiracles.—The term *spiracle* is held to include not only the external opening, and the annular sclerite or *peritreme* which surrounds it, but also the *atrium* or vestibule into which the opening leads, together with the *closing apparatus.* The latter consists of one or more muscles with associated cuticular parts. The atrium is a specialized region of the trachea leading from the spiracular opening: it lacks tænidia and its walls are variously sculptured or are provided with hairs, trabeculæ and similar chitinous outgrowths. Closely connected with the spiracles are frequently *peristigmatic glands* which secrete an oily or other material preventing the wetting of those organs. The structure of the spiracles presents an enormous range of variety among different groups of insects: it is also usually different in the thoracic and abdominal spiracles of the same insect and may be greatly modified in different instars. It will, therefore, be readily appreciated that their classification is a matter of much difficulty. Krancher (1881) divided spiracles into two main groups, viz., those without lips and those provided with lips. Under the latter category are included a number of subdivisions based upon various structural points. Mammen (1912) classified spiracles into four groups founded upon the number and relations of the muscles connected with the closing apparatus: his work, however, deals almost entirely with Hemiptera.

The most generalized type of spiracle is devoid of lips and closing apparatus and is little more than a simple crypt as in *Sminthurus*. No special chamber or atrium is developed and the spiracle opens directly into the tracheæ.

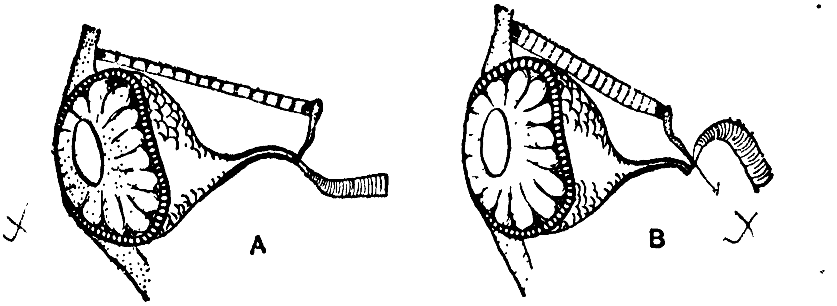

Fig. 114.—Spiracle and Occluding Apparatus of *Trichodectes*, Semidiagrammatic. *A*, open; *B*, closed. *After* Harrison, *Parasitology*, 1915.

In most Hemiptera, more especially in the abdomen, the spiracles are simple apertures surrounded by a peritreme. A well developed atrium is present and between the latter and the trachea is the closing apparatus. This type of spiracle is also found in the Anoplura, Aphaniptera and in other insects (Fig. 114).

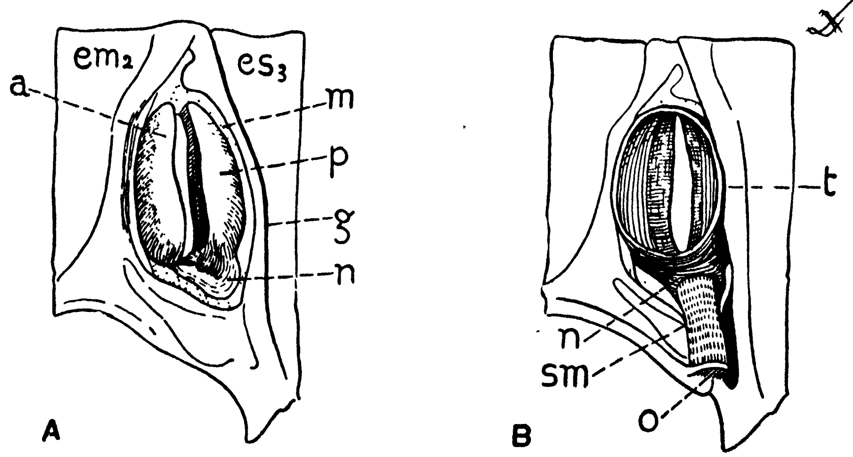

Fig. 115.—Metathoracic Spiracle of a Grasshopper (*Dissosteira*). *A*, outer view. *B*, inner view. em_2, mesepimeron; es_3, metepisternum; *g*, intersegmental fold; *m*, membrane; *t*, trachea. Further explanation in the text. Adapted from Snodgrass, 1929.

In grasshoppers the thoracic spiracles each have a slit-like opening guarded by two external valves or lips (Figs. 115 and 116, A). The metathoracic spiracles have movable lips (*a*, *p*) united by a ventral lobe (*n*): they open by their own elasticity but are closed by an occlusor muscle (*sm*) arising from a process (*o*) on the margin of the mesocoxal cavity. The abdominal spiracles (Fig. 116, B, C, D) have no projecting lips, the integument being inflected to form two hardened walls of the atrium—one wall (*v*) being movable and the other (*d*) is fixed. The movable wall is prolonged into a process or manubrium (*q*) to which the occlusor (*sm* 1) and opening muscles (*sm* 2) are attached.

In the spiracles of lepidopterous larvæ the lips are fringed with repeatedly branched processes, whose finest divisions often require a high magnification for their detection, thus forming a most efficient guarding mechanism to the tracheal system. At the inner end of the atrium is the closing apparatus. The latter consists of a chitinous bow, which partly encircles the trachea, while on the opposite side of the latter is a chitinous band ; a closing lever or rod is closely connected with the band. The occlusor muscle is attached at one end to the bow and at the other to the lever : when the muscle contracts the lever presses the band against the bow, thus closing the entrance into the trachea. The latter is opened partly by means of the elasticity of the chitinous parts which regain their former position, and partly by the aid of an antagonist muscle or an elastic fibre (Fig. 117).

In the larvæ of *Melolontha* and other of the Lamellicornia (Boas, *Zool. Anz.* 1893 : Meinert 1895) the spiracles are circular : each consists of a crescentic sieve-plate and a projecting tegumentary fold or bulla which is almost completely surrounded by it (Fig. 118). The true opening is a curved slit situated near the margin of the bulla and running concentrically with it. The sieve plate consists of an outer pore membrane supported beneath by a layer of trabeculæ (Fig. 119).

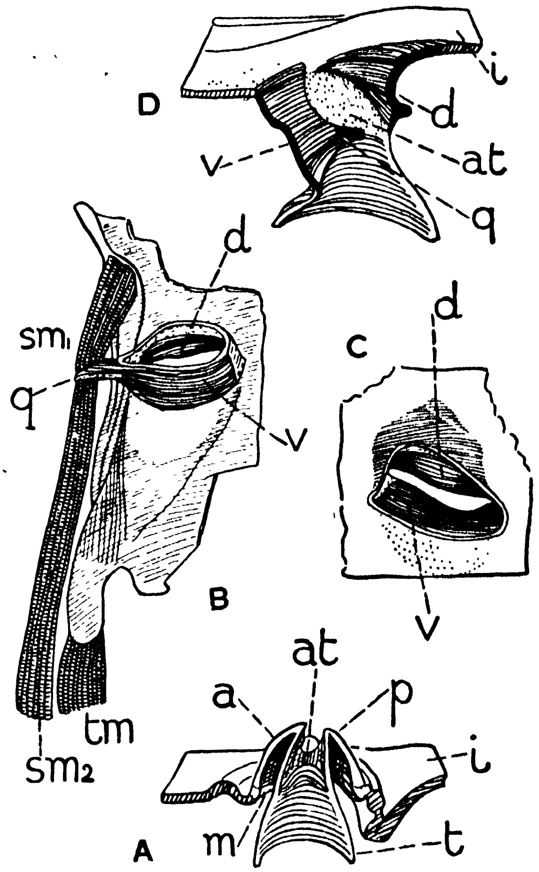

FIG. 116.—SPIRACLES OF A GRASSHOPPER (*DISSOSTEIRA*).

A, *D*, sections through metathoracic and 1st abdominal spiracles respectively. *B*, inner view, and *C*, outer view of 1st abdominal spiracle. *at*, atrium ; *i*, integument ; *tm*, tympanal muscles. Further explanation in the text. Adapted from Snodgrass, 1929.

In larvæ of the Elateridæ, Cleridæ, Nitidulidæ and other Coleoptera are *biforous spiracles.* Each has two contiguous openings which are more or less slit-like and separated by a partition wall. Each opening communicates either by means of a tubular passage with a common atrium, or opens directly into the trachea (Fig. 118). Other types of spiracles in larval Coleoptera are described by Steinke (1919).

In Dipterous larvæ the spiracles are without closing apparatus (vide de Meijere 1895, 1902). In the third-stage larvæ of the higher Cyclorrhapha the posterior spiracles consist of a pair of chitinous plates. Each plate is surrounded by a peritreme and bears as a rule three openings which may be pyriform (*Muscina*) or in the form of straight slits (*Calliphora*) or sinuous slits (*Musca*). Each opening is traversed by a number of fine chitinous rods presenting the appearance of a grating, and all three openings communicate with a common atrium. Just internal to the openings there

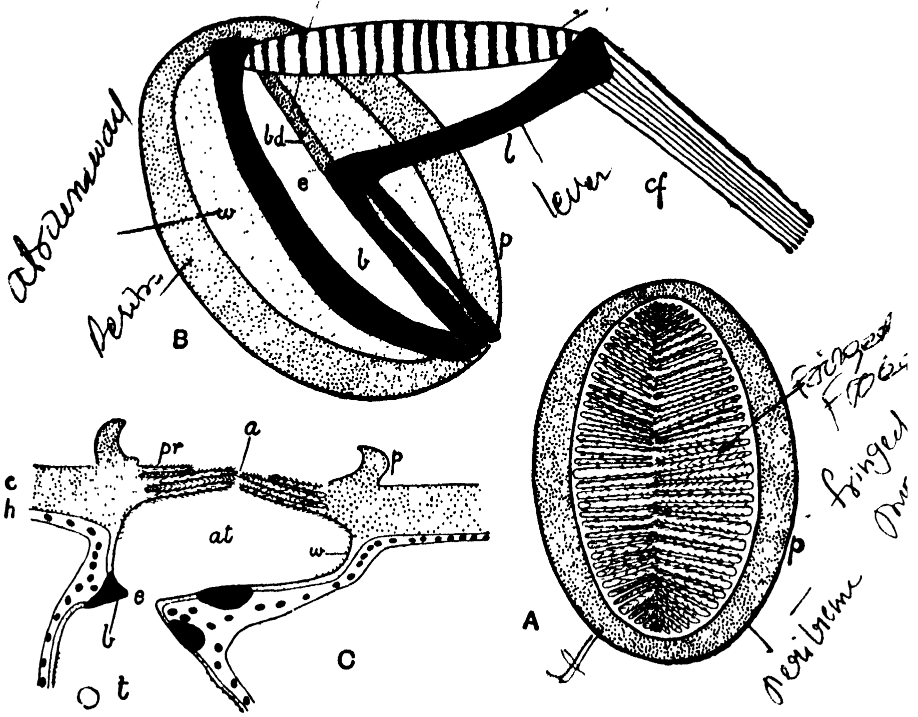

FIG. 117.—SPIRACLE OF A LEPIDOPTEROUS LARVA (*SPHINGIDÆ*).

A, seen from the outside showing fringed processes of the lips; *B*, seen from the inside, lips omitted; *C*, sectional view. *a*, spiracular aperture; *at*, atrium; *b*, bow; *bd*, band; *c*, cuticle; *cf*, elastic fibre which opens spiracle; *e*, entrance into trachea; *h*, hypodermis; *l*, lever; *p*, peritreme; *pr*, fringed processes of lips; *w*, wall of atrium; *t*, trachea.

is a system of branched chitinous trabeculæ which form, along with the grating previously alluded to, an efficient barrier to the entrance of foreign particles. The walls of the atrium are also lined with a fibrous reticulum.

The anterior spiracles each consists of a variable number of digitate processes whose apices are perforated by openings. Each opening communicates with a small atrium and the atria of each spiracle all join with the main tracheal trunk of their side. Since both anterior and posterior spiracles change in form at each instar the spiracles of the previous instar atrophy. The new larval or pupal spiracle arises as an outgrowth of the atrium which eventually meets the skin. The old atrium shrivels, only persisting as a stigmatic cord, and all that remains of the original spiracle is seen in the stigmatic scar or cicatrix (Figs. 121 and 130) found in close connection with the functional spiracle. In the larvæ of *Œstrus*, *Hypoderma* and other of the Œstridæ instead of three

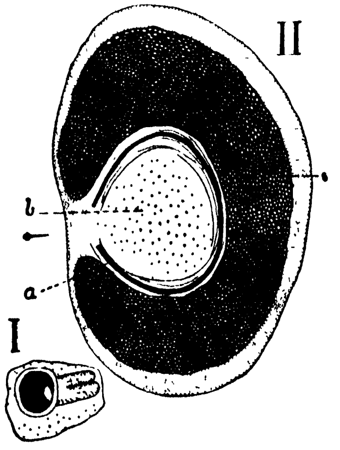

FIG. 118.—I. BIFOROUS SPIRACLE OF A CLERID LARVA. *After* Boving and Champlain. II. ABDOMINAL SPIRACLE OF THE LARVA OF *MELOLONTHA VULGARIS*.

a, spiracular opening; *b*, bulla; *s*, sieve plate. The arrow is directed anteriorly.

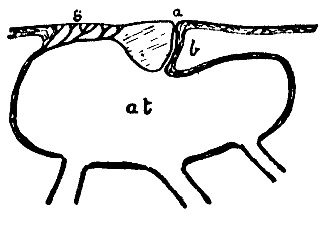

FIG. 119.—LONGITUDINAL SECTION OF A SPIRACLE OF THE LARVA OF *MELOLONTHA*.

at, atrium: other lettering as in Fig. 118.

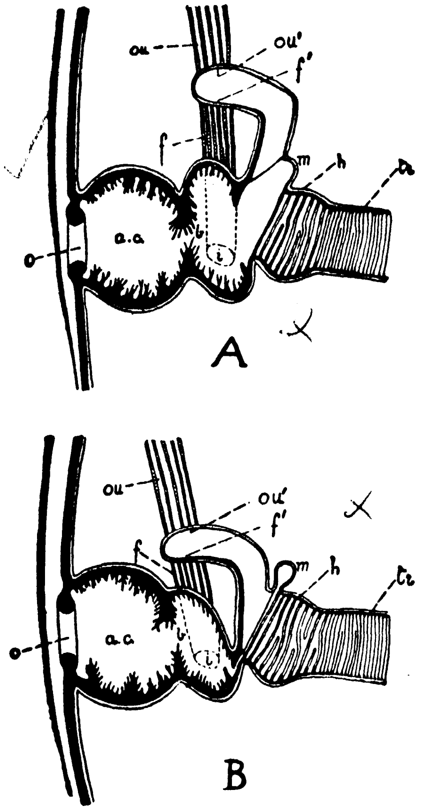

FIG. 120.—LONGITUDINAL SECTIONS OF THE LAST ABDOMINAL SPIRACLE OF AN ANT.

A, open; *B*, closed; *o*, spiracular opening; *a.c.*, anterior chamber; *b*, occluding chamber; *f*, closing muscle and f^1 mobile insertion of same; *h*, thickened portion of trachea; *i*, fixed insertion of closing muscle; *m*, flexible membrane; *o*, spiracular opening; *ou*, opening muscle; ou^1, fixed insertion of same; *tr*, trachea. *After* Janet, 1902.

openings to each spiracle there are multiple pores. In *Glossina* there are about 500 of these pores to a side which form the sculpturing on a pair of *polypneustic lobes* (Newstead, 1918). Each pore is connected by means of a tubular continuation with large tracheal trunks within the lobes. A similar arrangement obtains in the larva of *Hippobosca* except that the pores are much less numerous, while in *Melophagus* there are only four to each lobe.

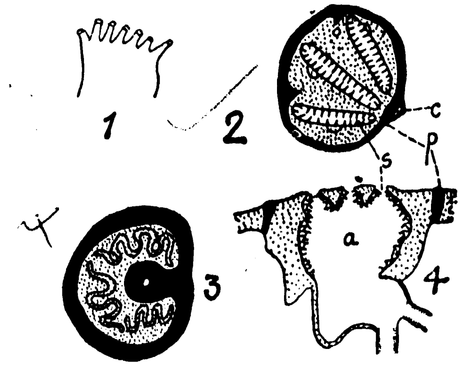

FIG. 121.—SPIRACLES OF LARVAL DIPTERA.

1, anterior spiracle of *Musca domestica*; 2, posterior spiracle of *Calliphora erythrocephala*; 3, posterior spiracle of *Musca domestica*; 4, vertical section through spiracle of *Calliphora*; chitinous parts only shown; *a*, atrium; *c*, cicatrix; *p*, peritreme; *s*, spiracular slit.

The Tracheæ and Tracheoles

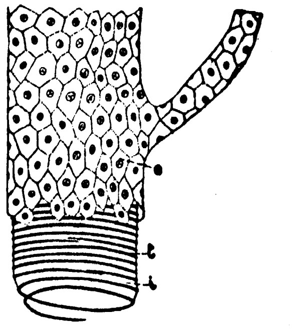

FIG. 122.—PORTION OF A TRACHEA STAINED WITH IRON-ALUM HÆMATOXYLIN. (Highly magnified.)

e, epithelial layer (ectotrachea); *i*, chitinous intima (endotrachea) with tænidium *t*.

The *tracheæ* are elastic tubes and when filled with air present a silvery appearance. The innermost lining of a trachea is a layer of chitin known as the *intima* (endotrachea) which is directly continuous with the cuticle of the body-wall and is cast off at each ecdysis. When examined microscopically a trachea presents a very characteristic striated appearance which is due to the fact that the intima is specially thickened at regular intervals to form closely arranged thread-like ridges which project into the lumen (Fig. 122). These bands or thickenings are known as *tænidia* and, as a general rule, they pass round the trachea in a spiral manner although their continuity is frequently interrupted: in other cases they form independent rings. The function of the tænidia is to keep the tracheæ distended and thereby allow of the free passage of air. If a trachea be teased out the intima will tear between the tænidia and the latter will uncoil after the fashion of an unwound wire. In some insects several tænidia exist side by side and in teased preparations a ribbon-like band uncoils which is formed of several parallel thickenings. Tænidia are absent, as a rule, from the large tracheæ close to the spiracles, the intima in such positions presenting a tesselated or other type of thickening. In some insects (*Zaitha, Lampyris, Luciola,* etc.) cuticular piliform processes arise from the tænidia and project into the cavity of the trachea (vide Stokes, 1893).

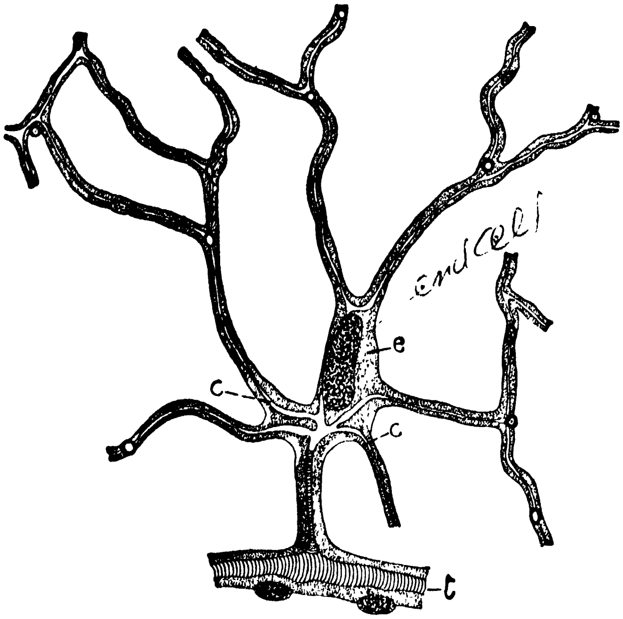

FIG. 123.—TRACHEAL END-CELL AND TRACHEOLES FROM THE SILK GLAND OF THE LARVA OF *PHALERA BUCEPHALA* (LEPIDOPTERA).

e, end cell; *c,* tracheoles; *t,* trachea. After Holmgren, *Festschr. Liljeborg,* 1896.

An epithelial layer (ectotrachea) lies outside the intima and is composed of pavement cells with relatively large nuclei. The larger tracheæ of some insects are faintly coloured with reddish-brown or violet pigment which is lodged in the cells of the epithelial layer. A delicate basement membrane forms the outermost coat of the tracheæ.

The ultimate branches of the tracheal system are termed *tracheoles.* These are extremely delicate intracellular canaliculi less than 1 μ in diameter and are always devoid of tænidia. As a rule they unite with their fellows to form a capillary reticulum whose minute structure has received diverse interpretations. It has been shown by Holmgren (1895) and others that the finer tracheal branches terminate in *end cells* or *transition cells* of a more or less stellate form (Fig. 123). Each tracheal branch is connected within a cell of this type with several tracheoles which pass to the cells of the particular tissue with which they are associated. The tracheoles penetrate within the cells of the salivary glands of Lepidoptera and Trichoptera: they also pass deeply into the ganglia of the nervous system, they enter between the fibres of the muscles and are found over the digestive system, Malpighian tubes and reproductive organs. In the fat-body of the larva of *Gastrophilus equi* the tracheoles lie wholly within the cytoplasm of exceptionally large tracheal cells of a special type (Prenant, 1900) containing hæmoglobin (Fig. 124).

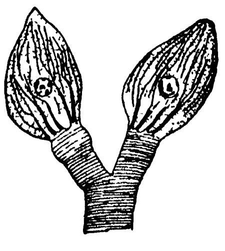

FIG. 124.—TRACHEAL CELLS FROM THE FAT-BODY OF A *GASTROPHILUS* LARVA.

The general arrangement and distribution of the tracheæ in the body of an insect presents important differences among various groups but, so far, no systematic study of the subject has been made. The researches of Fuller (1919) show that among the Isoptera the respiratory system of a newly-hatched termite consists of a framework of comparatively few simple tracheæ from which a multitude of dichotomizing, arborescent, and other tracheæ gradually develop and this statement holds good for the majority of insects. The specialization of the respiratory system, Fuller adds, is one of reduction, the nascent system of the more specialized termites being less extensive than that of the more generalized members.

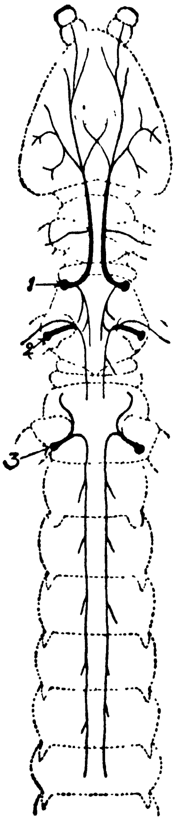

FIG. 125.—TRACHEAL SYSTEM OF *CAMPODEA*.

1, 2 and 3, SPIRACLES. *After* Grassi, 1887.

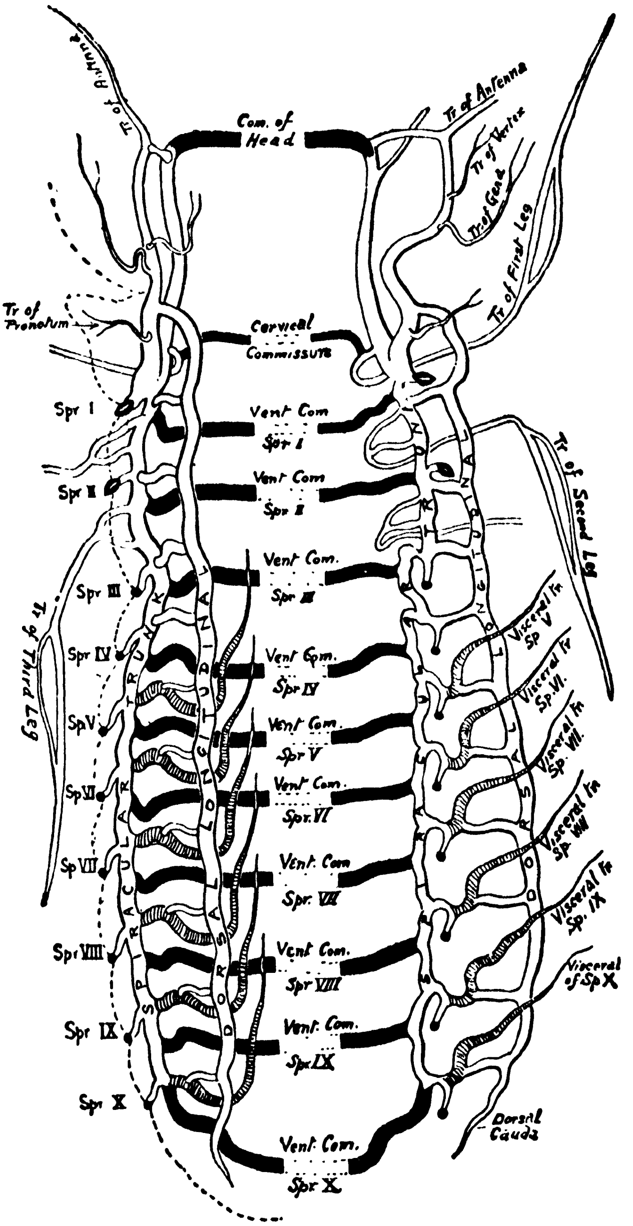

FIG. 126.—DIAGRAMMATIC REPRESENTATION OF THE TRACHEAL SYSTEM OF A NEWLY HATCHED NYMPH OF *TERMES NATALENSIS* AND OTHER SPECIES.

On the left as seen from above, on the right with the dorsal longitudinal trunk pushed aside. *After* Fuller, *Ann. Natal. Mus.*, 1919.

The work of Fuller will serve as a basis for similar ontogenetic and comparative studies in the absence of which no general conclusions are possible.

Each spiracle communicates with a short inwardly directed spiracular trachea which divides within its segment into branches passing to the various organs. In *Machilis* and *Campodea* Grassi (1887) has shown that the tracheæ associated with each spiracle form, in themselves, an independent system which has no anastomoses with the tracheæ from neighbouring spiracles (Fig. 125). In *Japyx solifugus* each spiracular trachea divides into an anterior and a posterior branch: since the anterior branch from one spiracle unites with the posterior branch from the spiracle in front a lateral spiracular trunk is formed on each side of the body. In *Nicoletia* and *Lepismina* these longitudinal trunks are also evident, but in addition there is a series of ventral, metameric, transverse commissures which unite the former trunks, thus combining the tracheæ of the two sides of the body into a single system. This condition is the normal one in many larvæ but in the imagines of the more generalized orders secondary longitudinal trunks are usually developed. Of these the most constant are the dorsal longitudinal trunks which are connected with the corresponding spiracular trunks by means of segmentally arranged palisade tracheæ (Fig. 126). In *Periplaneta,* certain of the Isoptera and other insects, a pair of ventral longitudinal trunks connect the segmental transverse commissures (Fig. 127).

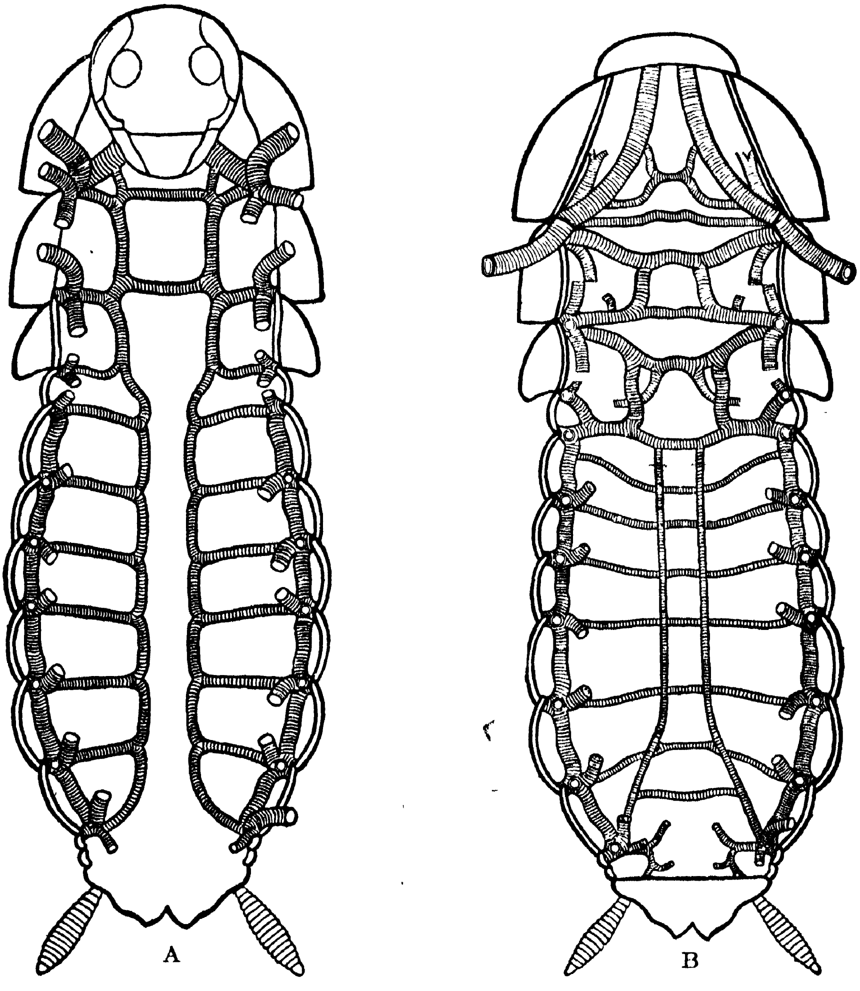

FIG. 127.—TRACHEAL SYSTEM OF *PERIPLANETA*.

A, with the ventral integument and viscera removed showing dorsal tracheæ; B, with dorsal integument and viscera removed showing ventral tracheæ. *After* Miall and Denny.

The dorsal longitudinal trunks give off segmental branches which pass to the heart and dorsal musculature. Visceral branches, which supply the digestive canal and reproductive organs, take their origin from the palisade tracheæ or directly from the spiracular tracheæ. The nerve cord and ventral musculature are supplied by branches derived from the ventral transverse commissures. The tracheæ supplying the legs arise from the spiracular (or, in Odonata, the dorsal) longitudinal trunks in the thoracic region, and the basal tracheæ of the developing wings usually take their origin in close association with those of the leg tracheæ of the meso- and meta-thorax (vide Comstock, 1918). The head and mouth-parts are principally supplied by branches derived from the main longitudinal trunks.

The Air-Sacs

In many winged insects the tracheæ are dilated in various parts of the body to form thin-walled vesicles or *air-sacs*. For the most part they are extremely delicate in structure and usually lack tænidia which ordinarily keep a tracheal tube open. The air-sacs are consequently distensible and, when inflated, are easily seen as glistening white vesicles. When collapsed and empty they are generally exceedingly difficult to detect. In *Melolontha*, for example, the air-sacs are dilatations of the secondary tracheæ and are relatively small in size but exceedingly numerous. In *Melanoplus* there are a pair of large thoracic air-sacs and five pairs in the abdomen which are likewise dilatations of the secondary tracheæ: there are also many smaller vesicles among the muscles. The air-sacs attain their greatest development in *Volucella*, *Musca* and other of the Cyclorrhapha and in *Apis* and *Bombus* among Hymenoptera (Fig. 128). In these instances the abdominal air-sacs attain very large dimensions and are dilatations of the main longitudinal tracheal trunks. Air-sacs are also met with among Lepidoptera and Odonata.

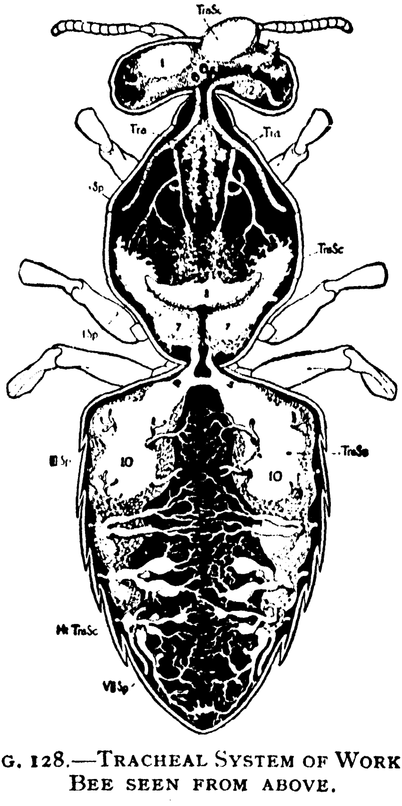

FIG. 128.—TRACHEAL SYSTEM OF WORKER BEE SEEN FROM ABOVE.

(One pair of Abdominal air-sacs removed and transverse ventral commissures of abdomen not shown.) The air-sacs (*Tra. Sc.*) are indicated in arabic numerals: *sp*, spiracles. *After* Snodgrass, *U.S. Bur. Entom. Tech. Ser.* No. 18.

It has been maintained by the earlier writers that the air-sacs lessen the specific gravity of the body during flight since when distended they slightly increase the volume of the body. The temperature of the air within the sacs is very little above that of the atmosphere outside and consequently the loss of weight due to inflation is negligible. It is, furthermore, counteracted by the slightly increased volume of the insect occasioning a proportionally greater resistance to the atmosphere during flight. The presence of air-sacs, on the other hand, allows of an increased supply of oxygen in the respiratory system and thus affords a greater breathing capacity. Insects with well-developed air-sacs are commonly swift of flight and their great muscular activity when on the wing demands an abundant air-supply in relation to the increased rapidity of respiration. A system of rapidly-filled storage reservoirs in close association with the muscles and other organs of the body would appear to meet this physiological demand.

In the marine Coleopteron *Æpus* a single pair of abdominal air-sacs is present These vesicles function as storage reservoirs which retain a supply of air during the time the insect is submerged (Miall).

In the aquatic larva of *Chaoborus* the main longitudinal tracheal trunks are strongly dilated into two pairs of sacs, one pair being located in the thorax and the other in the 7th abdominal segment. According to Franckenberg (1915) these vesicles are filled with oxygen (?) and function as hydrostatic organs. The insect adapts itself very rapidly to changes of pressure, requiring only a few minutes to adjust to an increase of two or three atmospheres.

The Gills or Branchiæ

Gills are special respiratory organs situated at localized positions on the body and are present in the immature stages of many aquatic insects. They are outgrowths of the integument or, in some cases, of the walls of the rectum and being in free communication with the general body-cavity they contain blood. The cuticle investing these organs is extremely thin and allows of the inward passage of oxygen by means of diffusion. Two types of gills are recognizable, viz., tracheal gills and blood-gills (Fig. 129).

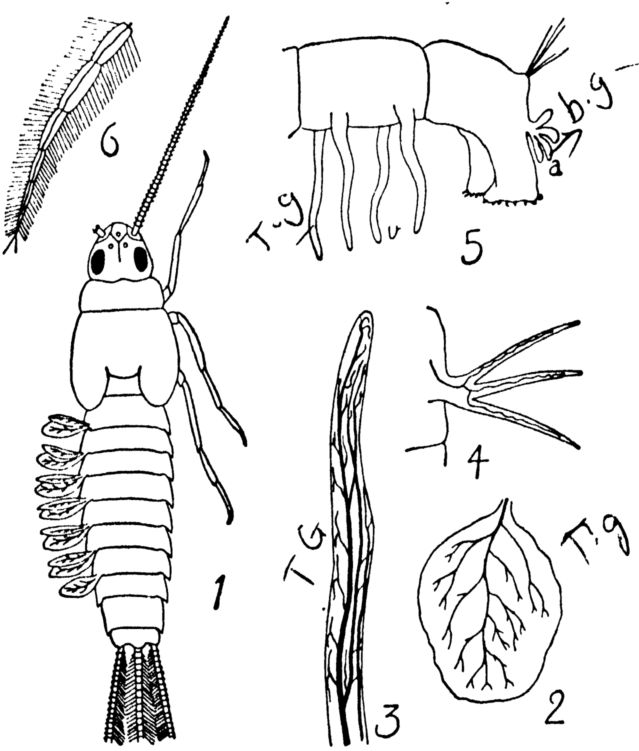

Fig. 129.—Gills of Aquatic Insects.

1, Nymph of *Chlœon* showing tracheal gills of left side; 2, 7th tracheal gill of *Chlœon* more highly magnified; 3, tracheal gill of a *Phryganea* larva; 4, tracheal gill of a larva of *Nymphula stratiolata*; 5, hind extremity of a larva of *Chironomus* showing anal blood gills (*a*) and ventral blood gills (*v*); 6, jointed tracheal gill of a larva of *Sialis*.

Tracheal Gills are filiform or more or less lamellate organs which are well supplied with tracheæ and tracheoles. They are present in the majority of aquatic larvæ and in some aquatic pupæ. In many cases they are the only organs of respiration but in others (larval Culicidæ for example) they are accessory in function and co-exist with open spiracles. Tracheal gills are usually borne on the abdomen: they are less frequently present on the thorax, and are only very rarely found on the head (*Jolia* and *Oligoneuria* among Ephemeroptera). In a few instances the gills of the larvæ persist throughout life in the imago: they are best exhibited in *Pteronarcys* whose imagines possess thirteen pairs of gill-tufts on the ventral surface of the thoracic and first two abdominal segments. Tracheal gills similarly persist in other Plecoptera and in *Hydropsyche* among Trichoptera but, as a rule, they are retained in a more or less shrivelled condition.

In the Ephemeroptera tracheal gills are usually borne on the first seven abdominal segments and may be either lamellate or filamentous in character. When lamellate each gill may consist of a simple leaf-like expansion (*Chlœon*) or the lamella may form a cover which protects a tuft of filamentous gills beneath (*Heptagenia*). In *Cænis* the upper lamellæ of the 2nd pair of gills form opercula which conceal and protect the gills behind. In *Prosopistoma* the gills are entirely hidden within a special branchial chamber.

In the Plecoptera primitive abdominal gills occur in the Eustheniidæ, but in the nymphs of other forms they are replaced by secondary tufts of filaments which are variable in position.

Tracheal gills are universally present in the nymphs of *Odonata*. In the Anisoptera they are in the form of an elaborate system of folds of the wall of the rectum, the latter chamber being modified to form what is termed the branchial basket. In most of the Zygoptera there are three external caudal gills and no rectal gills; in a few rare cases lateral filamentous abdominal gills are also present.

Among Neuroptera gills are present in the larvæ of the Sialoidea and in *Sisyra* among the Plannipennia. They consist of seven or eight pairs of filaments, usually jointed, borne segmentally on the abdomen.

Filamentous abdominal gills are present in the majority of larval Trichoptera and frequently persist in the pupæ of those insects. In some genera although the larvæ are gill-less the pupæ are provided with well developed branchial organs.

Among Lepidoptera tracheal gills have long been known in the larva of *Nymphula* (*Paraponyx*) *stratiolata*); they consist of a series of delicate filaments arising from the sides of the trunk segments.

Among coleopterous larvæ tracheal gills are filamentous in character and are only present in a few of the families. In *Pelobius* they are ventral and are located near the bases of each of the pairs of legs and on the first three abdominal segments. In the Gyrinidæ there are 10 pairs of hair-fringed lateral abdominal gills; somewhat similar organs are also found in *Hydrocharis* and *Berosus* among the Hydrophilidæ. In *Cnemidotus* they take the form of numerous elongate jointed filaments which arise from the dorsal surface of the thorax and abdomen. In *Psephenus* there are five pairs of tufted ventral abdominal gills and in *Psephenoides* there is a single retractile tuft of anal gills.

Among dipterous larvæ there are four lamellate anal gills in the Culicidæ; in *Phalacrocera* the tracheal gills are in the form of numerous elongate filamentous processes which arise from almost all parts of the body segments; in *Simulium* and *Eristalis* rectal gills are present.

Blood-gills are commonly tubular or digitiform and are sometimes eversible. They derive their name from the fact that they contain blood but not as a rule tracheæ, although occasional tracheoles may be present. In some instances there is little real distinction between these organs and tracheal gills. Blood-gills are of infrequent occurrence and are not exclusively confined to aquatic insects. They are found among many larval Trichoptera which have 4 to 6 finger-like tubes at the anal extremity. Among Diptera they are well developed in the larvæ of *Chironomus*, some species of which bear two pairs of ventral blood-gills on the penultimate segment, and a group of four shorter anal gills. Small anal blood-gills are also met with among aquatic Tipulid larvæ and, according to Pantel, in larvæ of several genera of Tachinidæ. The ventral eversible sacs of the Thysanura are probably also of the nature of blood-gills.

Types of Respiratory System

Three morphological types of respiratory system are recognized among insects (vide Palmen, 1877: Gryse, 1926).

(1) **The Holopneustic Respiratory System.**—In this type, which is the primitive one, all the spiracles are open: they are borne on the meso- and meta-thorax and on the first eight abdominal segments. The holopneustic condition is the prevalent one in the imagines of many orders

of insects, also in the greater number of the nymphs and in larvæ of many Hymenoptera and of *Bibio* among Diptera.

(2) **The Hemipneustic Respiratory System.**—This type is derived from the holopneustic condition by the closure of one or more pairs of spiracles and is the prevalent one among larvæ. The following terms are in use which indicate the distribution of the spiracles.

Peripneustic.—Spiracles in a row along each side of the body. In typical examples the prothoracic and abdominal spiracles are open, those of the wing-bearing segments being closed. This condition is found in the larvæ of the orders Neuroptera, Mecoptera, Lepidoptera, of many Hymenoptera Symphyta, and of many Coleoptera; among Diptera it is prevalent in larvæ of the Bibionidæ, Mycetophilidæ and Cecidomyidæ.

Amphipneustic.—Only the prothoracic and the posterior abdominal spiracles are open. This type is the usual one among larval Diptera.

Propneustic.—Only the prothoracic spiracles are open. A comparatively rare condition exhibited for example in the pupæ of the Culicidæ.

Metapneustic.—Only the last pair of abdominal spiracles are open. The prevalent type in larval Culicidæ and Tipulidæ and in *Hypoderma* among the Œstridæ; also found in the first larval instar of most Cyclorrhapha and in the aquatic larvæ of certain Coleoptera (Dytiscidæ, Hydrophilidæ, etc.).

In addition to the foregoing there are certain anomalous types which do not obviously fall under any of the above categories. In *Campodea*, for example, there are only three pairs of spiracles which are located on the thorax, while in certain of the Protura and many Coccidæ the number is reduced to two pairs which are similarly thoracic in position. Among the Thysanoptera there are one or two pairs of thoracic spiracles and a pair on the first and eighth abdominal segments. In *Sminthurus* there is only a single pair of spiracles which is located on the cervical region. It is convenient to group these specialized examples under a separate category which may be termed the *oligopneustic* type.

(3) **The Apneustic Respiratory System.**—In this type of respiratory system oxygenation of the tissues is effected by osmosis either through the general integument, which in such cases is thin and membranous, or by means of gills. The spiracles are either closed or totally wanting. Respiration through the general surface of the integument takes place throughout life in almost all Collembola and among certain of the Protura. It also occurs in the larva of the Dipteron *Chaoborus* and in the early instars of endoparasitic hymenopterous larvæ. Respiration by means of gills prevails among the immature stages of many aquatic insects.

Although the tracheal system is well developed in most apneustic insects, it is greatly reduced in larval Chironomidæ and totally absent in almost all Collembola and in the family Acerentomidæ among Protura.

The Stigmatic Cords

In many hemipneustic and apneustic insect larvæ the spiracular branches are in the condition of delicate strands or *stigmatic cords.* They pass from the lateral longitudinal trunks to points on the cuticle where spiracles if present would be located or where their scar-like vestiges occur. The existence of these cords affords support to the conclusion that the closed or partially closed tracheal system is a derivative from an ancestral holopneustic condition. Stigmatic cords have been detected in larvæ of most orders of insects.

Physiology of Respiration

Among vertebrates it is well known that oxygen is conveyed to the tissues by means of the hæmoglobin in the blood, but in the vast majority of insects it is primarily conveyed to the various organs of the body by the tracheal system. The blood in these animals is generally of secondary importance in respiration, but it is incorrect to assert, as is stated in some works, that it plays no part in the process at all. The whole subject of insect respiration, and the literature thereon, is discussed by Wigglesworth (1931), and the reader is referred to his paper for more detailed information.

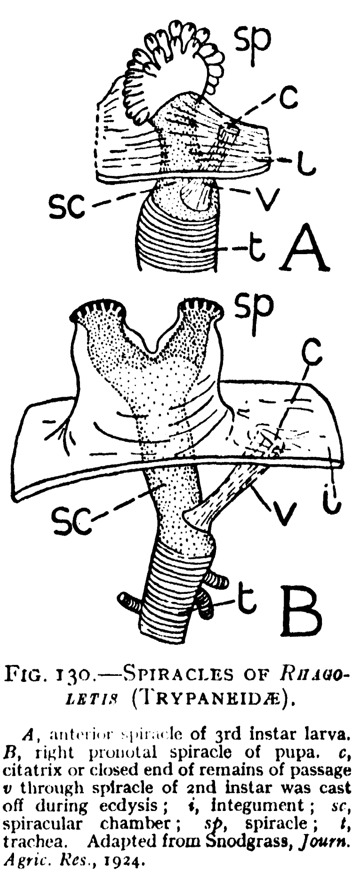

FIG. 130.—SPIRACLES OF *RHAGOLETIS* (TRYPANEIDÆ).

A, anterior spiracle of 3rd instar larva. *B*, right pronotal spiracle of pupa. *c*, citatrix or closed end of remains of passage *v* through spiracle of 2nd instar was cast off during ecdysis; *i*, integument; *sc*, spiracular chamber; *sp*, spiracle; *t*, trachea. Adapted from Snodgrass, *Journ. Agric. Res.*, 1924.

In holo- and hemi-pneustic insects the air enters the tracheal system through the spiracles and is either continuously changed by the physical process of gas diffusion, or rhythmically changed by muscular movements of the body-wall, in combination with diffusion. Among most larvæ, in pupæ and in the smaller and less active imaginal forms, diffusion alone prevails. In the larger and more active imagines respiratory movements are a regular phenomenon. Expiration is brought about by the contraction of the tergo-sternal and other of the body muscles which bring the terga and sterna closer together. Inspiration is not, as a rule, produced solely by the elasticity of the body shields causing return to their normal positions, but is caused by the contraction of special muscles which separate the terga and sterna. Most of what is known concerning the respiratory movements of insects is due to Rathke (1860), Plateau (1884) and Langendorf (1883). The two last-mentioned observers, by means of lantern projections on a screen, studied the enlarged silhouettes of the insects under investigation (Fig. 131). By this method the changes of contour due to inspiration and expiration were observed and traced upon the screen so as to give two superposed figures. The principal facts concerning the respiratory movements of an insect at rest, as determined by this method, may be summarized as follows.

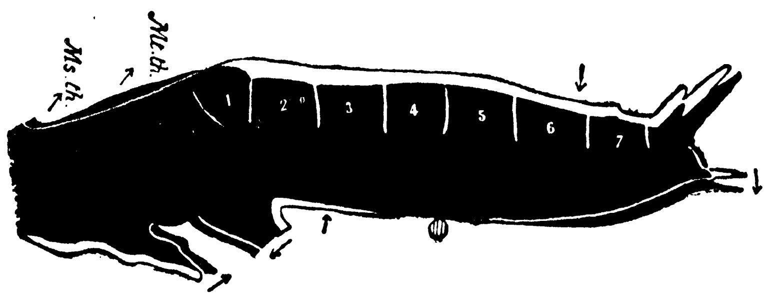

FIG. 131.—PROFILE OF *BLATTA ORIENTALIS*.

The black surface represents the expiratory contour, the thin line the inspiratory contour. The arrows show the direction of the expiratory movement. *After* Plateau; reduced from a magic-lantern projection.

(1) The respiratory movements of insects are located in the abdomen and, in most cases, the thoracic segments do not participate. *Blatta orientalis*, however, is an exception in this respect.

(2) The movements consist of an alternate contraction and recovery of the figure of the abdomen in two dimensions, viz., vertical and horizontal. During expiration both diameters are reduced while during inspiration they revert to their previous condition. The vertical expiratory contraction is the most marked and in *Periplaneta* amounts to ⅛th of the depth of the abdomen (between segments 2 and 3). Changes in the length of the abdomen involving protrusion and subsequent retraction of the segments are rare in insects as a class, but are characteristic of aculeate Hymenoptera.

(3) The nature of the respiratory movements depends upon the formation of the abdominal segments. In Coleoptera the sterna yield but little while the terga are mobile; in *Periplaneta* the sterna are slightly raised during expiration. When the terga overlap the sterna and conceal the pleural membrane, the two shields approach and recede alternately, the sterna being the more mobile. This type of movement is exhibited in Odonata, acrydian Orthoptera, aculeate Hymenoptera and Diptera. When the pleural membrane is freely exposed the terga and sterna approach and recede alternately, the pleural region becoming at the same time depressed and then returning to its original figure. This type is prevalent among Tettigoniidæ, Neuroptera, Trichoptera and Lepidoptera.

(4) In most insects the expiratory movement is active and is effected by the contraction of certain of the abdominal muscles; inspiration is slower than expiration and is partially effected by the elasticity of the body-wall.

(5) The frequency of the respiratory movements depends upon temperature and the muscular activity of the insect.

Notwithstanding the very definite nature of the respiratory movements, their significance is not fully understood. By alternately dilating and compressing the tracheæ they bring about ventilation of the larger vessels in a way analogous with the respiratory movements of mammals. The fact that the tracheæ are for the most part circular in cross-section and provided with spiral thickenings to prevent collapse, argues that they are not easily compressed. In some insects, however, the main tubes are elliptical in cross-section, or have imperfect spiral thickenings, and are consequently compressible. In others, the development of an elaborate system of air-sacs allows of compression. It is not clear whether respiratory movements cause a simple flow of gases in and out of the tracheæ or whether a directed current is involved. Certain recent experiments with Orthoptera suggest that the thoracic spiracles are inspiratory and those of the abdomen expiratory. Whether such differentiation of spiracular function is constant, or dependent upon an internal mechanism regulating the action of the spiracular valves according to varying needs, is still uncertain (vide also p. 69). According to Krogh (1920) the tracheal system in *Dytiscus* is emptied during strong expiration of two-thirds of its total gas capacity, the remainder being changed by diffusion. The latter process is of prime importance in tracheal respiration, and in insects which show no respiratory movements the whole of the gaseous exchange takes place by this process. In all insects gaseous exchange in the smaller tracheæ and the tracheoles is by means of diffusion. As Krogh has shown, the diffusion of oxygen into the tracheal system may be determined by the formula

$$S = \frac{k\,(p - p')\,A}{L}$$

where S = c.c. of oxygen used per second; p = partial pressure of oxygen in the atmosphere (20·93 per cent. of an atmosphere); p' = partial pressure of oxygen at the ends of the tracheæ; A, the mean cross-sectional area of the tracheæ in cm^2; L, the mean length of the tracheæ in cm., and k = the diffusion constant for oxygen (i.e. = 0·18). By means of this formula it can be shown that diffusion provides an adequate supply of oxygen to the tissues and maintains at the tracheal endings a partial pressure of oxygen of only 2 per cent. to 3 per cent. below that in the outside air. Whether the air penetrates to the utmost limits of the tracheoles or whether the ends of the latter contain liquid has been much discussed. According to Wigglesworth (1930) a variable amount of fluid occupies the ends of the tracheoles which is controlled by the osmotic pressure exerted by the surrounding tissue fluids. Since the osmotic pressure increases during muscular activity, for instance, liquid will be absorbed from the tracheoles and air will replace it. In this way the surface from which oxygen can diffuse into the tissue fluids will be correspondingly increased.

While the intake of oxygen is through the spiracles the elimination of carbon dioxide presents certain special problems. While being given off from the tissues it will diffuse in all directions and pass to the exterior partly through the integument and partly by means of the tracheal system. The proportion of carbon dioxide that will escape via the integument naturally depends upon the permeability of the latter, the strength and frequency of the respiratory movements and other factors. Thorpe (1928) has shown that in insects with thin cuticle carbon dioxide escapes from the general body surface, whereas in heavily sclerotized Coleoptera it only diffuses through the intersegmental membranes. Few exact measurements of the proportion of carbon dioxide that is eliminated through the general-body cuticle have been made. According to v. Buddenbrock and Rohr (1922 A) it amounts in *Dixippus* to about 25 per cent. of the total output.

In aquatic insects, with a closed tracheal system, the principle involved in the respiratory exchange is the diffusion of gases in solution through an intervening membrane. In most cases the membrane concerned is the thin integumentary covering of the gills or, where the latter organs are wanting, the diffusion takes place through the general body-wall. In water with normal oxygenation the oxygen content of the tracheal air is lower than that of the water, whereas the CO_2 content is the same as or a little higher than that of the surrounding water. The oxygen dissolved in the water passes by diffusion through the part of the integument concerned and enters the tracheæ in the gaseous state. Here it is circulated, partly by body movements and partly by diffusion, into the tracheoles from which it passes again into solution in the protoplasm of the tissues and in the blood. As the internal oxygen is constantly being used up in respiration there is a continuous diffusion from the region of higher partial pressure (in the water) to the region of lower partial pressure (in the insect) and the gases tend to equilibrate. In insects devoid of a tracheal system, or where the latter is only very feebly developed, the oxygen diffuses directly into the blood which conveys it to the various organs. In apneustic parasitic larvæ which live bathed in the blood of their host, the only available source of oxygen is that contained in the latter. Since the host breathes atmospheric oxygen its blood would contain a higher percentage of oxygen than that of the parasite, and the same principle of diffusion from a region of higher partial pressure (maintained in the blood of the host) to one of lower partial pressure (in the blood of the parasite) would hold good. It is noteworthy that the cuticle of these parasites has an extreme tenuity, and there is frequently a subcutaneous reticulum of fine tracheæ which is in accordance with this type of cutaneous respiration. In many of the Apterygota, which are terrestrial organisms, the cuticle is also but little chitinized and a tracheal system is totally wanting. In these cases oxygen is believed to diffuse through the general surface of the body and to be taken up by the blood which acts as the sole distributing agent. No general respiratory protein, comparable with hæmocyanin in Crustacea, has been discovered among insects. The blood has been found to contain but little oxygen and no more than can be accounted for by physical solution. There is little doubt, however, that the blood plays the part of intermediary between the tracheolar endings and many of the tissues, while in atracheate forms it acts as the sole oxygen carrier. In many metapneustic dipterous larvæ a rich supply of tracheal branches passes to the hindmost chamber of the heart forming, apparently, as a kind of lung. In a few exceptional cases hæmoglobin is present. Thus among certain *Chironomus* larvæ it occurs in the blood plasma and such forms live in an environment poor in oxygen. As Leitch (1916) has shown, this pigment enables the blood to bind chemically sufficient oxygen for the needs of the animal when the oxygen tension of the surrounding medium becomes too low for the necessary supply to be provided by physical solution. Hæmoglobin also occurs in specialized tracheal cells of *Gastrophilus* larvæ (Fig. 124); in somewhat similar cells in the Notonectids *Buenoa* and *Anisops* and in the male accessory genital gland of *Macrocorixa* (Haviland Brindley).

There is reason to believe that the intracellular respiratory pigment termed *cytochrome* (Keilin, 1925) is of general occurrence among insects, and its presence indicates that they already possess the chief constituents from which hæmoglobin may arise. The existence of hæmoglobin, therefore, in these isolated instances does not necessarily imply any profound physiological difference between them and other insects devoid of this pigment.

Cytochrome is found in highest concentration in the thoracic muscles of flying insects, a fact which appears to be correlated with the rich tracheal supply, peculiar structure, and exceptional activity of the wing-muscles (vide p. 55). The facility with which cytochrome constantly takes up oxygen and supplies it to the cells suggests that its high concentration is to meet the oxygen requirements of these special muscles. In other organs and tissues it has been detected only in small amounts, while it has also been found in both eggs and larvæ.

Literature on the Respiratory System and Respiration

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THE CIRCULATORY SYSTEM

AMONG insects the circulatory system is largely an open one, there being only a single closed organ or dorsal vessel. The greater part of the circulation of the blood takes place in the cavities of the body and its appendages, the blood occupying the spaces not appropriated by the internal organs. The larger of these spaces may be enclosed by special membranes and form definite sinuses. With the exception of the aorta-like anterior prolongation of the dorsal vessel, which usually divides into terminal branches, there are as a rule no definite veins or arteries such as are found in many Arthropoda. In the appendages and wing-veins, however, the blood flows in ingoing and outgoing streams along defined channels analogous to blood-vessels. In the larva of *Chlœon* the hindmost chamber of the heart gives off three caudal arteries which enter the respective tail appendages.

The organs and tissues belonging to the circulatory system are separately dealt with below.

The Diaphragms and Sinuses.—When the diaphragms are completely developed the general body-cavity or hæmocœle is divided into three sinuses by means of two fibro-muscular septa (Fig. 132). The *dorsal diaphragm* is the principal septum and the one most generally prevalent. It extends across the abdominal cavity above the alimentary canal and the blood-space, thus enclosed, is known as the *dorsal* or *pericardial sinus.* The latter is situated beneath the abdominal terga and within it is located the heart. The *ventral diaphragm* stretches across the abdominal cavity just above the ganglia of the ventral nerve cord, and the space limited by it is the *ventral* or *perineural sinus.* Between the dorsal and ventral sinuses is the large central cavity or *visceral sinus* containing the principal internal organs.

Pairs of *alary muscles*, composed of striated fibres, arise from the terga and spread out fanwise over the surface of the dorsal diaphragm. The fibres of one alary muscle meet, beneath the heart, those of the corresponding muscle of the opposite side of the body. In some insects, including the Collembola, dipterous larvæ, and Anoplura, the alary muscles are attached to the walls of the heart (Fig. 134). These muscles vary in number, largely according to the number of chambers present in the heart. In *Periplaneta*, for example, there are 12 pairs of alary muscles (Fig. 133) in the hive bee 4 pairs, in *Hæmatopinus* 3 pairs and in the larva of *Chironomus* 2 pairs.

The Dorsal Vessel.—The dorsal vessel extends from near the caudal extremity of the body, through the thorax, and terminates in the head. It is situated along the median dorsal line just beneath the integument and is protected by the dorsal diaphragm below. Morphologically it is a continuous tube, usually closed posteriorly, and always open at its cephalic extremity. It is divisible in two regions, viz., the *heart* or pumping organ and a conducting vessel or *aorta.*

The *heart* is maintained in position within the pericardial sinus by means of suspensory filaments attached to the abdominal terga and frequently to the dorsal diaphragm also. It is generally divided by successive constrictions into a series of chambers but, in some insects, it is an unconstricted tube, and its segmentation is only evidenced by the presence of paired ostia (described below). In the most primitive condition there is a chamber for each thoracic segment, and for each segment of the abdomen, excepting the last. Among most insects, however, the heart is restricted to the abdomen and is variously shortened from both extremities with the result that the chambers are fewer in number than the abdominal segments. In *Periplaneta* (Fig. 133) the heart is exhibited in an exceptionally primitive condition and is composed of thirteen chambers: in *Japyx* there are ten chambers, in *Lucanus cervus* seven, among aculeate Hymenoptera there are five, and in *Musca* three: in a few insects the heart is reduced to only one chamber. Histologically the heart is composed of a single layer of cells with large nuclei, and striated muscle fibrillæ are differentiated within the cytoplasm. The cellular layer is bounded both externally and internally by a delicate membranous tunic. The blood enters the heart through lateral inlets or *ostia*, a pair of which is situated at each constriction between adjacent chambers. The wall of the heart is reflected inwards and forwards at each ostium to form an *auricular valve*, which precludes the

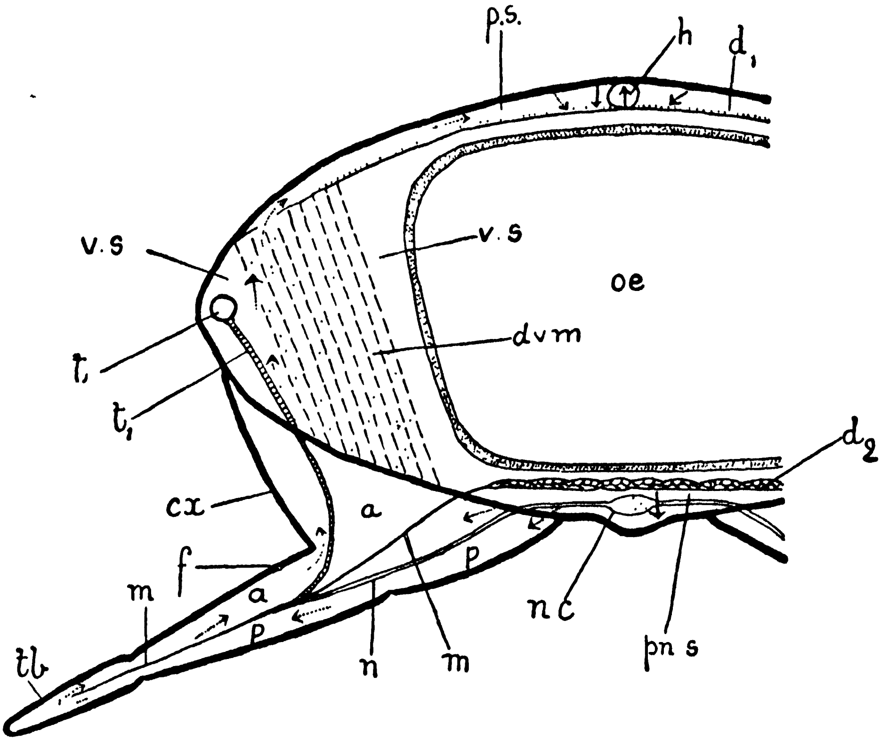

FIG. 132.—SCHEMATIC TRANSVERSE SECTION OF THE THORAX OF *PERIPLANETA* SHOWING THE DIAPHRAGMS AND SINUSES.

The plain arrows indicate the course of the circulation towards the head and the dotted arrows signify transverse currents more or less parallel with the plane of the paper. *h*, dorsal vessel; *d*, pericardial diaphragm; *p.s.*, pericardial sinus; *œ*, œsophagus; *v.s*, visceral sinus; *dvm*, dorso-ventral muscles; *t*, lateral tracheal trunk; t_1, leg trachea; d_2, ventral diaphragm; *pn.s*, peri-neural sinus; *nc*, nerve cord; *n*, nerve to leg. The cavity of the leg is divided into an anterior sinus *a* and a posterior sinus *p* either by muscles or by a membrane *m*; in the femur the trachea and nerve are attached to the membrane; *cx*, coxa; *tb*, tibia and tarsus. Adapted from Brocher, *Ann. Soc. Ent. Fr.* 1922.

return flow of the blood into the dorsal sinus. In many insects each pair of auricular valves also functions as a ventricular valve, which prevents the backward flow of the blood in the heart itself (Fig. 137). In the larva of *Æschna* the ventricular valves are separately developed and situated some distance in front of each pair of ostia.

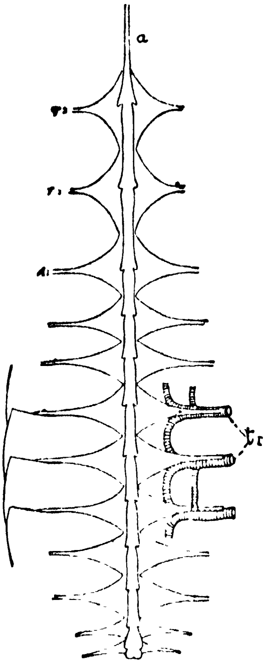

FIG. 133.—DORSAL VESSEL WITH ALARY MUSCLES OF *PERIPLANETA* SEEN VENTRALLY.

a, aorta ; T_2, T_3, A_1, alary muscles attached to the terga of the 2nd and 3rd thoracic and 1st abdominal segments; *tr*, tracheal arches. *After* Miall and Denny.

The *aorta* is the anterior prolongation of the dorsal vessel and it functions as the principal artery of the body. Its junction with the heart is frequently marked by the presence of *aortic valves*. The aorta extends forwards through the thorax to terminate in the head near the brain. In some insects its anterior extremity is an open funnel-like mouth but, more usually, it divides into two or more *cephalic arteries*, each of which may subdivide into smaller vessels.

Accessory Pulsatory Organs.—In addition to the heart accessory pulsatory organs have been described in many insects. They are sac-like structures, situated in various regions of the body, and pulsate independently of the heart. Brocher (1919) has observed thoracic pulsatile organs in *Protoparce* and *Dytiscus* where they are present just beneath the meso- and metathoracic terga. In *Protoparce* the mesotergal pulsatile organ is well developed and is directly connected with a special diverticulum from the loop of the aorta (Fig. 135) : the metathoracic organ, on the other hand, is very small. In *Dytiscus* the reverse obtains, the metathoracic organ being the best developed. Among Hemiptera special pulsatile organs are present in the legs : in *Periplaneta* and other insects, including Lepidoptera, there is a pulsatile vesicle at the base of each antenna.

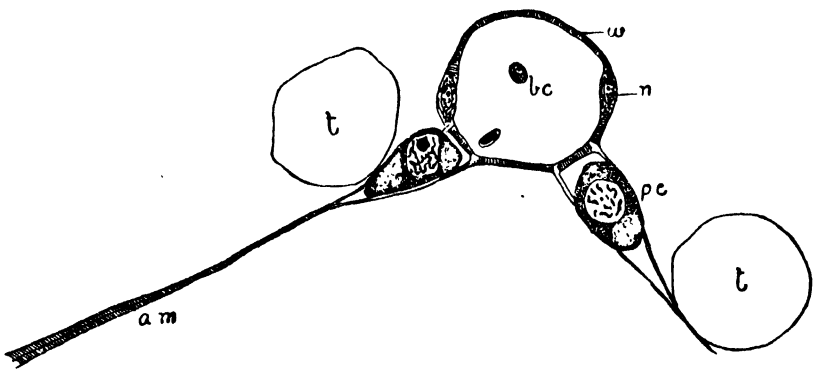

FIG. 134.—TRANSVERSE SECTION OF THE HEART OF A TACHINID LARVA.

bc, blood corpuscles ; *w*, wall of heart ; *n*, nucleus ; *am*, alary muscle ; *pc*, pericardial nephrocyte ; *t*, trachea. *After* Pantel, *La Cellule*, 1898.

The **Blood.**—The blood (or hæmolymph) of insects is contained in the general body-cavity, where it freely bathes the various internal organs and also enters the appendages and the tubular cavities of the wing-veins.

It consists of a liquid substance or *plasma* containing a number of small amœboid, nucleated, colourless corpuscles known as *leucocytes* or *amœbocytes* which vary in diameter between about ·006 mm. and ·027 mm.

The plasma may be either colourless or pale yellow, green, reddish, etc., owing to certain dissolved pigmentary substances which combine with the proteids present. In the larvæ of some species of *Chironomus* the plasma is red owing to the occurrence of hæmoglobin. Among leaf-eating lepidopterous larvæ, Poulton and others have shown that the yellow and green pigments of the blood are derived from the food, and absorbed without undergoing fundamental changes. When in contact with the air the blood frequently darkens. This change is due to two causes:—(1) the oxidation of the albuminoid substances present and (2) the precipitation of greenish-black granules of uranidine which is produced at the moment the blood leaves the insect (Cuénot). Clotting is also a frequent phenomenon, the clot involving both the leucocytes and uranidine granules.

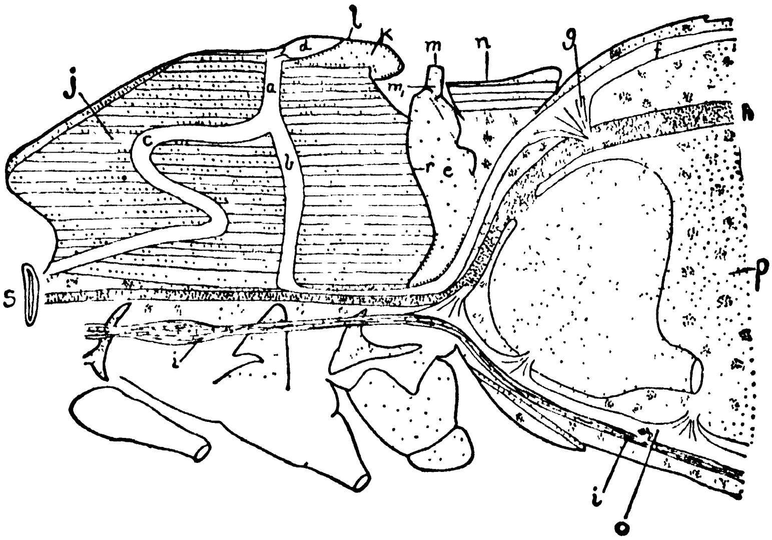

FIG. 135.—SECTION THROUGH THE THORAX AND BASE OF THE ABDOMEN OF *PROTOPARCE CONVOLVULI* SHOWING THE CIRCULATORY SYSTEM (DIAGRAMMATIC).

a, branch of aorta to mesothoracic pulsatile organ *d*; *b,c*, loop of aorta; *e* and *k*, air-sacs; *f*, heart; *g*, alary muscle; *h*, gut; *i*, ventral nerve cord; *j*, mesotergal muscles; *l*, scutellum; *m*, metatergum and its pulsatile organ m_1; *n*, 1st abdominal tegum; *o*, ventral diagram; *p*, blood space; *r*, mesophragma; *s*, spiracle. Adapted from Brocher, *Arch. Zool. Exp.* 1919.

The more recent researches have shown that marked differences exist in the blood of the two sexes. Thus Steche (*Zeits. indukt. Abstamm. u. Vererb.* 8, 1912) observed that the plasma of male larvæ of *Lymantria dispar* is yellowish and that of the female green. Also, when the plasma of the two sexes is brought together a precipitin is formed. These experiments have been extended by Geyer (*Zeits. wiss. Zool.* 105, 1913) who noted a similar precipitin reaction in other insects, including cases where no colour differences occur in the plasma of the two sexes.

The *leucocytes* exist in several forms and four types of these cells are recognized by Hollande (1911) as being present in most insects (Fig. 124). These are—(1) *Proleucocytes* or young leucocytes which divide by mitosis and give rise to the other types of leucocytes. (2) *Phagocytes* or cells capable of ingesting other tissues and microörganisms: such cells have a hyaline protoplasm; (3) *Granular leucocytes* whose protoplasm is charged with granules exhibiting acidophile or basophile reactions: these cells frequently function as phagocytes. (4) *Œnocytoids*, rounded or spherical cells which do not exhibit phagocytosis: their protoplasm is homogeneous and markedly acidophile. Hollande's classification of the leucocytes differs from that of Cuenot (1895) who regards (2) and (3) as stages in the evolution of a single type of cell. In addition to the foregoing elements there may be special leucocytes charged with fat (Heteroptera) or wax (*Orthezia* and many Aphididæ).

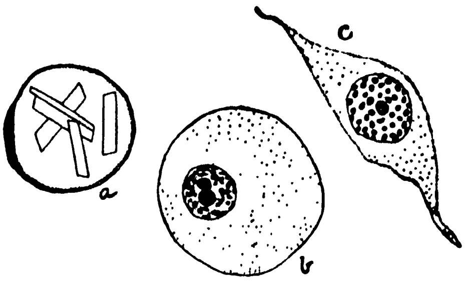

FIG. 136.—BLOOD CORPUSCLES HIGHLY MAGNIFIED.

a, wax cell of *Aphis chrysanthemi*; *b*, œnocytoid from larva of *Psylliodes napi*; *c*, phagocyte of *Zygæna trifolii*. *After* Hollande, *Arch. Zool. Exp.* 1911.

The principal function of the blood is the transportation of the nutritive products of digestion to the various organs of the body. Its rôle in respiration in most insects is secondary owing to the highly developed tracheal system which conveys oxygen to all parts of the organism. (For the respiratory function of the blood vide p. 130)

Certain insects exhibit the property of reflex-bleeding or, in other words, they have the power of ejecting blood from the femoro-tibial and other articulations of the body. They usually feign death at the time, and the blood which exudes may possess toxic, caustic or other properties which it is believed render such insects distasteful to their enemies. Reflex-bleeding is particularly evident in *Melöe*, *Cantharis* and other Coleoptera, also in certain Hemiptera and Orthoptera, while many Aphididæ discharge blood through their cornicles.

The Circulation of the Blood.—The heart is the principal pulsatory organ, and it undergoes rhythmical contractions which are brought about by the muscle fibrillæ situated in its walls. When the heart is composed of several chambers the latter pulsate, one after the other, with the result that a peristaltic wave of contraction passes from the caudal extremity forwards. At the moment of diastole, in a given chamber, the blood enters through the ostia from the pericardial sinus, but the ventricular valve is closed. During systole, this valve is open, and the blood flows into the chamber in front: at the same time the ostia are closed, and the return of the blood into the pericardial sinus is thus precluded (Fig. 137). On being propelled forwards, the blood passes out at the anterior end of the dorsal vessel, and enters the cavity of the head: from there it flows into the visceral and perineural sinuses. According to Brocher, the dorsal pulsatory organs bring about the circulation of the blood in the legs, wing-veins and among the muscles of the thorax. In *Protoparce convolvuli* he regards the mesotergal pulsatile organs as being more important than the heart in pumping the blood. By means of the up and down movements of the diaphragms its further circulation is provided for, and the blood ultimately returns to the pericardial sinus. It either enters through the

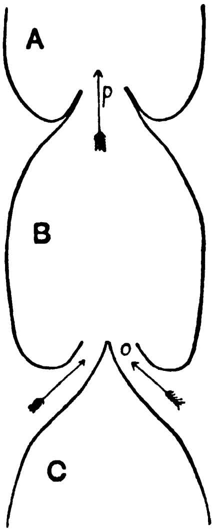

FIG. 137.—VALVES OF THE HEART.

A, B, C, chambers of the heart; AB, at the moment of systole; BC, at the moment of diastole. *p*, interventricular passage; *o*, ostium.

fenestræ in the dorsal diaphragm or, if these perforations are wanting, it flows into the pericardial sinus at the hinder extremity of the body, where the dorsal diaphragm is incomplete. The contractions of the body muscles during respiration are also of considerable importance in aiding the flow of the blood. The blood circulates in the veins of the expanding wings of newly emerged insects, and it is largely by means of the pressure which it exerts that these organs attain their full extension. The veins of the fully formed wings have been shown by Moseley (1871) and Brocher (1916, 1919, 1920) to function as blood channels since a definite circulation is maintained through them.

The frequency of the pulsations of the heart varies not only in different insects, but also in different stages in the ontogeny of the same species. In *Sphinx ligustri*, for example, Newport found that the average number of pulsations in a larva before the 1st ecdysis is 82–83 per minute, before the 2nd ecdysis 89, but before each succeeding ecdysis it gradually diminishes to 39 in the final larval instar: the force of the circulation intensifies as the number of pulsations diminish. During the quiescent period, prior to each ecdysis, the number of beats averages 30. In the pupa it falls to 22, and subsequently to 10 or 12, ultimately almost ceasing during hibernation. When the imago is in repose the pulsations number 41–50 and in flight 119–139. A decrease in temperature has a marked effect in reducing the frequency of the heart beats. Dogiel (1877) has found that in the larva of *Chaoborus* many poisons, when acting feebly, accelerate the pulsations, but when allowed to act energetically a retardation is exhibited. Such drugs as muscarine, curare and strychnine have no appreciable influence.

Special Organs and Tissues Associated with the Blood.—The following organs and tissues are regarded as performing important functions in connection with the blood. It must be pointed out, however, that their true physiological significance is still obscure and very divergent views are held.

THE CORPORA ALLATA.—These are a pair of small ovoid whitish bodies lying behind the supra-œsophageal ganglion, in close relation with the sympathetic nervous system (Fig. 62). In some cases they have been mistaken for a pair of posterior sympathetic ganglia but, histologically, they differ from nervous tissues and have rather the features of glandular organs (Fig. 138). According to Janet (1899) they develop as a pair of ectodermal invaginations of the mandibular segment. Physiologically, they are to be regarded as ductless glands which secrete certain substances (hormones ?) into the blood. Corpora allata are found in all orders of insects (vide Nabert, 1913).

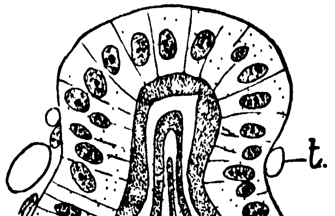

FIG. 138.—TRANSVERSE SECTION OF A CORPUS ALLATUM OF A PHASMID (*BACILLUS ROSSI*) SHOWING CONCENTRIC LAMELLÆ WITH EPITHELIAL COVERING.

n, nerve; *t*, trachea. *After* Heymons, *Sitz. Acad. wiss. Berlin*, 1899.

THE ŒNOCYTES.—The term œnocytes is given to certain usually very large cells, which are commonly grouped in metamerically arranged clusters in the pleural region of the abdomen or, occasionally, they may extend over the sterna (vide Wheeler, 1892). They are probably universal in all orders of the Pterygota and are ectodermal in origin, being derived from segmental groups of cells situated just behind the primary invaginations which give rise to the abdominal spiracles (Fig. 140). Among nymphal and larval insects the œnocytes may retain their original connection with the hypodermis, or they may migrate into the superficial layer of the fat-body, or come to lie in close association with certain of the branches of the tracheæ (Fig. 139). Among larval Culicidæ and Chironomidæ there are regularly two kinds of these cells—the large and small œnocytes. In adult insects the œnocytes often differ considerably from those of the immature stages of the same species. In the imagines of *Xiphidium* and *Blatta* they lose their original metameric arrangement and exhibit a more scattered distribution: in ants the œnocytes attain an enormously greater size in the larva than in the imago (Perez).

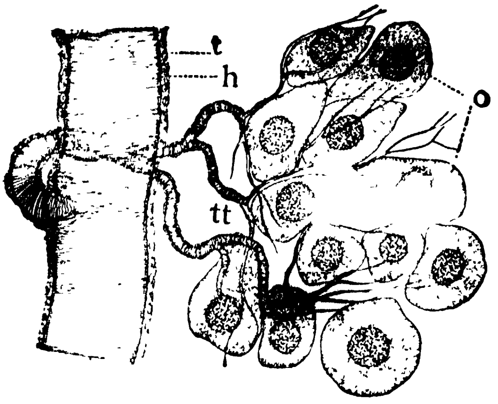

FIG. 139.—CLUSTER OF ŒNOCYTES FROM A NEARLY MATURE PHRYGANEID LARVA.

o, œnocytes; *t*, trachea; *tt*, small tracheal branches; *h*, tracheal hypodermis.

Histologically, an œnocyte is characterized by the large oval or rounded nucleus, an abundant cytoplasm, and an external limiting membrane. Œnocytes are variable in colour and often have the light yellow appearance of certain wines, a fact which suggested their name. The views held with regard to the functions of these cells are extremely conflicting, but it appears probable that they elaborate and discharge into the blood some physiologically important secretion. Glaser (1912) concludes from a series of experiments that in larvæ of *Zeuzera* they secrete enzymes which oxidize reserve food material stored up as fat.

THE PHAGOCYTIC OR SPLENIC ORGANS.—In *Forficula*, and some Orthoptera and Thysanura, Kowalevsky (1894) recognized certain bilateral groups of cells placed either just below the pericardial cells on either side (*Forficula*) or on the concave side of the dorsal diaphragm (*Caloptenus*). These cells exhibit a marked amœboid character and are believed to give rise to fresh leucocytes. It appears that they also have the property of taking up and storing particles of indian ink and other colouring matter when injected in suspension into the body cavity. In this respect they differ from nephrocytes which only deal with material in solution.

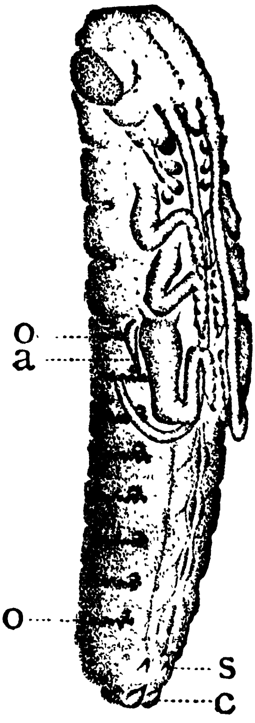

FIG. 140.—A NEARLY MATURE EMBRYO OF *XIPHIDIUM*.

o, œnocyte cluster; *a*, appendage of 1st abdominal segment; *s*, style; *c*, cercus. This and Fig. 127 after Wheeler, *Psyche*, 1892.

Literature on the Circulatory System and Associated Tissues

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THE EXCRETORY ORGANS AND FAT-BODY

THE principal excretory organs are the Malpighian tubes, and an accessory excretory function is performed by the nephrocytes, fat-body, and labial glands (in Thysanura).

The **Malpighian Tubes** (Fig. 141).—First discovered by the Italian anatomist Malpighi, these organs are almost universally present among insects. They are long, slender, blind tubes lying in the hæmocœl where they are freely bathed by the blood. They open at their proximal extremities into the commencement of the hind intestine, near the junction with the mid-gut. Distally, they are usually free but in some insects, particularly Coleoptera, their blind ends are closely attached to the walls of the colon or rectum without, however, opening into those chambers (vide Woods, 1916). The exterior of the Malpighian tubes is richly supplied with a reticulum of fine tracheæ whose larger branches serve to maintain these organs in position. The number of Malpighian tubes is very variable but tolerably constant within the limits of most of the orders (vide Veneziani, 1905). These vessels usually occur in twos, or multiples of two,

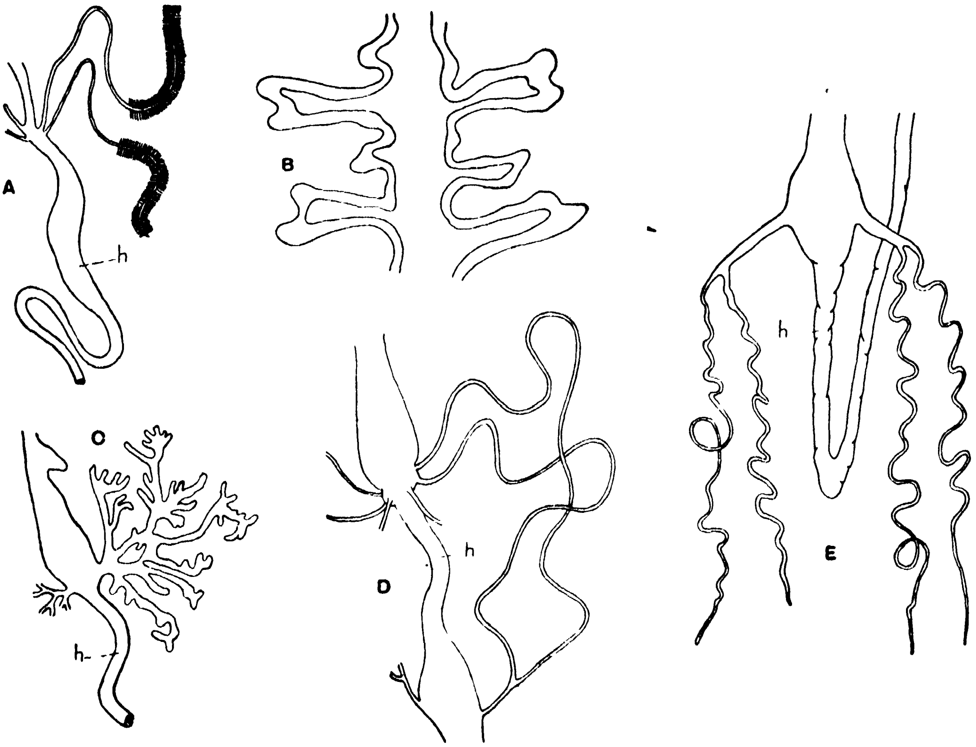

FIG. 141.—MALPIGHIAN TUBES.

A, *Melolontha vulgaris*. B, portion with diverticula more highly magnified. C, *Galleria mellonella*. D, *Timarcha tenebricosa*. E, *Calliphora* (larva). *h*, hind intestine. A—D *after* Veneziani, *Redia*, 1904.

and their primitive number according to Wheeler (1893) is six. It is only very exceptionally that more than six are present in the embryo and they are often reduced to four. Specialization either by addition or reduction is frequent: their number may exceed 100 while, on the other hand, it is often less than six. The typical number of these vessels present in the various orders is given below.

Anoplura, Thysanoptera, Hemiptera, Diptera and Aphaniptera 4.
Psocoptera, Coleoptera 4–6: Isoptera 2–8. Thysanura 4–16.
Mecoptera, Trichoptera and Lepidoptera 6. Neuroptera 6–8. Dermaptera 8–20.
Epemeroptera 8–100. Plecoptera 50–60. Odonata 50–70. Orthoptera 30–120.
Hymenoptera, 6–20 in ants and over 100 in many Aculeata.

The Coccidæ and larval parasitic Hymenoptera are exceptional in having only two Malpighian tubes and the Culicidæ have the unusual number of five. In certain of the Thysanura, the Protura, and Stepsiptera these vessels are doubtfully represented by papillæ: in the Collembola, *Japyx*, and the Aphididæ they are wanting altogether. Although the Malpighian vessels are usually simple tubes they are sometimes arborescent, as in *Galleria mellonella*, or they may give off short closely-packed diverticula as in *Melolontha* (Fig. 141). Very frequently the tubes unite in pairs and they may open into a common ampulla or bladder, which discharges into the hind intestine. When very numerous the Malpighian tubes may be grouped in bunches, each bunch discharging by a separate duct or ureter: in the *Gryllidæ* all the tubes converge to open into a common ureter of considerable length. Not infrequently the Malpighian tubes exhibit morphological and physiological differences. Thus, in *Haltica* and *Donacia* four of the tubes discharge into a common ampulla while the remaining two shorter vessels have isolated insertions. In the larva of *Myriatropa* the two posterior tubes are filiform while the distal portions of the anterior pair are of even greater diameter than the intestine and contain $CaCO_3$ which is absent in the other vessels.

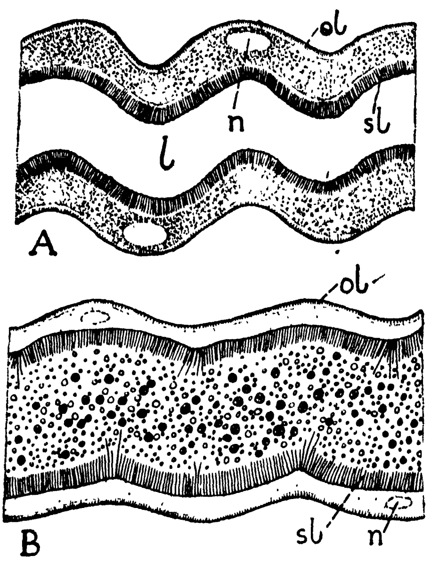

Fig. 142.—Malpighian Tubes of *Rhodnius* (Reduviidæ) seen in Optical Sections of Living Material. A, Upper Region of Tube with Excretory Granules in the Cells. B, Lower Region of Tube with Excretory Spheres in the Lumen.

l, lumen; *n*, nucleus of excretory cell; *ol*, outer striated zone; *sl*, inner striated margin (filamentous in B). Adapted from Wigglesworth, *Journ. Exp. Biol.* 1931.

When viewed in transverse section a Malpighian tube is seen to be composed of a ring of about three to eight large and variably-shaped epithelial cells with prominent nuclei. Histologically these cells bear marked resemblances to those of the convoluted tubules of the vertebrate kidney. Where each cell borders the cavity of the tube its margin exhibits a striated appearance whose true nature has been much discussed. In some cases it is due to numerous separate filaments while in others closely set pore canals appear to be responsible. The appearance may vary over different regions of each Malpighian tube (Fig. 142). The epithelial cells also show an outer striated zone in many insects and they rest externally on a basement membrane which is covered by a peritoneal coat often containing muscle fibres (Veneziani).

Functionally, the Malpighian tubes are concerned with the removal of the waste products of metabolism from the blood. These substances accumulate in the epithelial cells of the vessels and are discharged into the central cavities, thence they pass into the intestine and are evacuated through the anus. The waste products stated to be eliminated by the Malpighian tubes are extremely varied and naturally depend upon the character of the food. As a rule the Malpighian tubes are coloured yellow or brown but the nature of the pigment present is obscure. The chief products of protein metabolism are uric acid and its salts: other organic constituents are small quantities of creatine and sometimes of urea, while guanin, so characteristic of Arachnida, is absent. Of inorganic constituents the most important in many insects is calcium carbonate, while calcium oxalate is also frequent. Many other inorganic compounds, derived from the food and not being required by the organism, are excreted. The discharge of waste substances from the Malpighian tubes is facilitated by the vermiform movements sometimes seen in the latter which are due to the contraction of muscle fibres previously alluded to. Among Homoptera carbohydrates in the form of excess of sugars are regularly voided as "honey dew," of which they are the chief constituent.

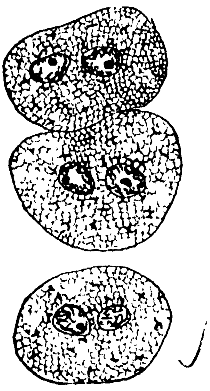

FIG. 143.—THREE VENTRAL NEPHROCYTES FROM THE LARVA OF *MELANOCHELIA RIPARIA*, HIGHLY MAGNIFIED.

After Keilin, *Parasitology*, 1917.

Calcium carbonate is known to occur in the Malpighian tubes of many saprophagous and phytophagous larvæ of the Diptera and also in certain larval Cerambycidæ. It is usually present in the form of small granules, but, in the Agromyzidæ, it forms calcospherites which also occur in special cells of the fat-body. Among Diptera, before pupation, the lime is dissolved in the blood and is excreted through the newly formed pupal cuticle into the ecdysial fluid. When the latter is absorbed the lime remains as a deposit on the inner surface of the puparium (Keilin, 1921). Among the Cerambycidæ the lime is utilized in the formation of an operculum which closes the pupal cell.

In the Carabid *Lebia scapularis* (Silvestri, 1905) and the Neuroptera Planipennia (Anthony, 1902) the Malpighian tubes secrete the silk used in constructing the cocoons, discharging it through the anus.

The **Nephrocytes** (Fig. 144).—The nephrocytes consist of certain localized groups of cells, often binucleate, which have the property of storing up substances of an excretory nature (Fig. 143). They occur in two principal groups: (1) the dorsal or pericardial nephrocytes and (2) the ventral nephrocytes. The dorsal nephrocytes are commonly termed the pericardial cells, which consist of two chains of cells arranged in a linear series one on either side of the heart in the pericardial sinus. Such cells are present in the immature stages and adults of most insects but in *Pediculus* they are represented by disseminated cell aggregates linked with the fat-body (Keilin and Nuttall). The ventral nephrocytes principally occur in Dipterous larvæ where they constitute the "garland-like cell-chain" of Weismann. In these insects they usually form a chain of cells which is suspended in the body-cavity below the fore-intestine and attached by its two extremities to the salivary glands.

The generally accepted opinion is that the nephrocytes are excretory in function. Hollande (1916), however, disputes this view and maintains that the pericardial nephrocytes absorb albuminoid substances of alimentary origin and render them assimilable. The excretory function of the nephrocytes is suggested by the fact that they have the property of taking up and storing ammonia-carmine and other dyes in solution when the latter are artificially introduced either directly by injection into the body-cavity or indirectly through the alimentary canal. Further information regarding the nephrocytes will be found in the writings of Kowalevsky (1886, 1889), Bruntz (1903), Cuénot (1986), Keilin (1917) and Keilin and Nuttall (1921).

The labial glands of the Thysanura discharge by means of an excretory duct which opens at the base of the labium. According to Bruntz (1908) these organs consist of a saccule which eliminates ammonia-carmine and a labyrinth which similarly deals with indigo-carmine when these substances are injected into the body-cavity.

The excretory function of the fat-body is discussed in the next section.

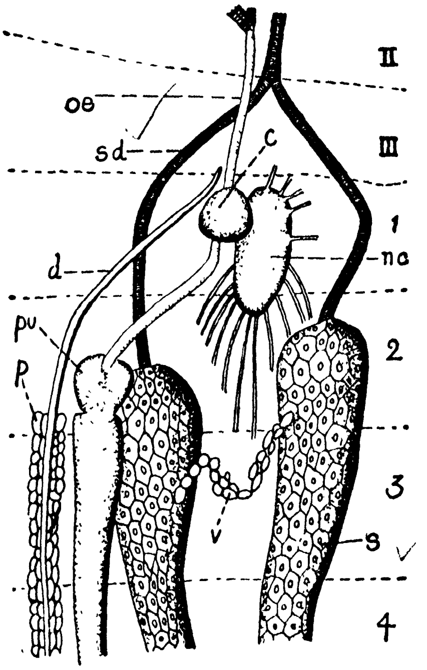

Fig. 144.—Dissection of the Anterior Region of the Larva of *Phaonia cincta* (Anthomyidæ), showing the Pericardial Nephrocytes *p*, and the Ventral Nephrocytes *v*.

II, III, 2nd and 3rd thoracic segments; 1–4, abdominal segments; *c*, cerebral ganglion; *d*, dorsal vessel; *nc*, ventral ganglionic centre; *œ*, œsophagus; *pv*, proventriculus; *s*, salivary gland; *sd*, salivary duct. Adapted from Keilin, *Parasitology*, 1917.

The Fat-Body

The fat-body is composed of irregular masses or lobes of rounded or polyhedral cells which are usually vacuolated and contain inclusions of various kinds. In many insects the fat-body is built up of tightly compacted cells: in others it is a more or less laminate tissue with numerous lacunæ, or it may take the form of loose strands. In colour it may be either white, yellow, orange or greenish. This tissue is derived from the mesoderm by a differentiation of the walls of the cœlomic cavities and it consequently has a primitive metameric disposition. With the breaking down of the embryonic cœlom, and the development of a hæmocœl, the fat-body forms the irregular boundaries of the permanent body-cavity. In many insects it is possible to distinguish an outer or *parietal layer*, beneath the body-wall, and an inner or *visceral layer*, which surrounds and enters between the various organs (Fig. 145). In some larvæ the parietal layer is interrupted at each segment and thus retains a segmental arrangement: the visceral layer, on the other hand, forms a continuous sheet passing from one segment to another. The fat-body alters very much in its histological structure during the life of an insect. In the earlier instars its nuclei are rounded or oval (Fig. 146, 3) but they often later alter in character, becoming stellate or ribband-like (Fig. 146, 2 and 4). In many cases the cellular structure is no longer evident and the fat-body has the appearance of a syncytium (Fig. 146, 1).

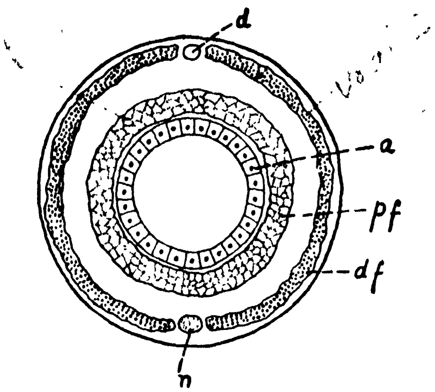

FIG. 145.—SCHEMATIC TRANSVERSE SECTION OF AN INSECT LARVA SHOWING DISTRIBUTION OF THE FAT-BODY.

a, alimentary canal; *d*, dorsal vessel; *n*, ventral nerve cord; *pf*, *df*, proximal and distal layers of fat-body.

The physiological processes associated with the fat-body are obscure. The latter is everywhere in direct communication with the blood, from which it receives and stores up the nutrient products of digestion, over and above those necessary to maintain the normal life of the organism. The most generally present substance is fat which accumulates in the form of globules in the vacuoles of the cells. Among other products albuminoid granules and glycogen are commonly found in numerous insects. Waste material in the form of urates is also deposited in the fat-body and when present in considerable quantity it imparts a greenish appearance to that tissue. In some insects the urates are found in the ordinary adipose cells, in others they are located in special *urate cells* (Orthoptera, Hymenoptera). Berlese has shown that in many larvæ the urates tend to accumulate in the parietal fat-body while the visceral fat-body stores up more especially albuminoid substances. As a rule the fat-body is most developed in larvæ, and the stores of nutrient material which accumulate in its cells are liberated during histogenesis. The reserves contained in the fat-body of adult insects are drawn upon during the reproductive processes: towards the end of the life of the organism the fat-body is greatly shrunken and reduced. Insects which hibernate possess a copious fat-body whose stores of nutriment are gradually absorbed during the quiescent period.

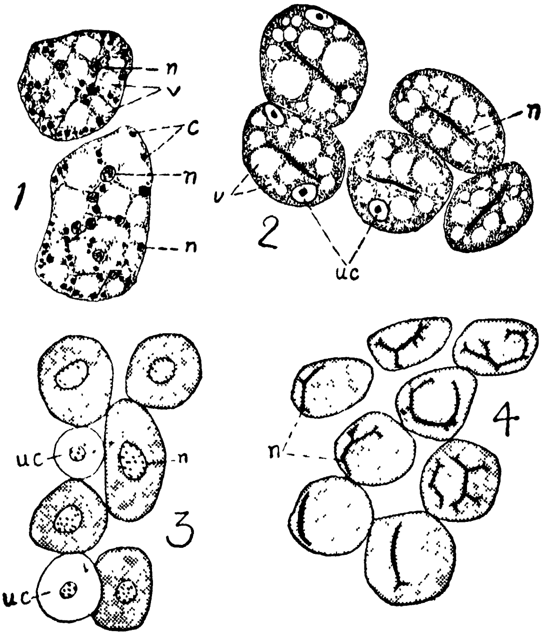

FIG. 146.—FAT-BODY OF VARIOUS INSECTS.

1, Adult Termite (soldier); 2, Adult larva of *Caliroa limacina*. 3, Young larva of *Formica rufa*. 4, Adult larva of same. *c*, urate concretions; *n*, nucleus; *uc*, urate cells; *v*, vacuoles filled with fat globules. Nos. 3 and 4 adapted from Pérez, *Bull. Sci. Fr. et Belg.*, 37.

The presence of urates indicates that the fat-body performs an important part in excretion and any excess of waste substances not dealt with by the usual excretory organs accumulates in its cells. In the Collembola, which have no Malpighian tubes, the fat-body becomes loaded with concretions of urates which increase in size and number with the age of the organism. In insects with complete metamorphosis, the urates, accumulated in the fat-body during the larval and pupal stages, are discharged through the alimentary canal at the time of emergence of the imago, and form the greater part of the meconium. In the Muscidæ, where the Malpighian tubes undergo re-formation in the pupa, their function is undertaken by the fat-body which becomes, temporarily, the principal organ of excretion (Marchal, Pérez).

Literature on the Excretory Organs and Fat-Body

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Vide also the chapter on Metamorphosis.

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THE GLANDS OR ORGANS OF SECRETION

THE glands of insects are composed of one or more cells which secrete a substance, or substances, to be used in or eliminated from the body. The essential elements of a gland are the epithelial cells which have the property of selecting from the blood those constituents which serve to build up the secretion.

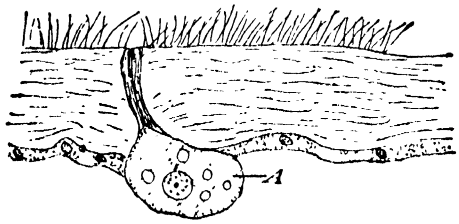

FIG. 147.—SECTION OF THE INTEGUMENT OF THE LARVA OF *ULA MACROPTERA* MG. (TIPULIDÆ) SHOWING UNICELLULAR HYPODERMAL GLAND (A).

After Keilin, *Arch. Zool. Exp.*, 1913.

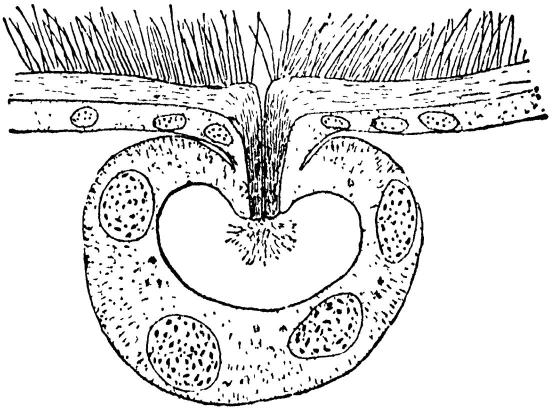

FIG. 148.—SECTION OF THE INTEGUMENT OF THE LARVA OF *GNOPHOMYIA TRIPUDIANS* BERG., SHOWING SIMPLE PLURICELLUAR GLAND.

After Keilin, 1913.

The most elementary types of glands are either unicellular or, if pluricellular, they are little more than simple aggregations of single units (Figs. 147, 148). Glands of this type are distributed in the integument of various parts of the body, and their secretions are discharged either directly to the exterior, or by means of separate ducteoles. In the larger or "organized" glands the secretory cells are disposed in the form of an epithelium bounding a tube, pit, or a more complex cavity. The secretion is discharged into the latter, and flows out through an efferent passage or duct, which opens on to the part of the body concerned by an aperture or pore. Such glands occupy very definite positions and are often of complex structure. According to their general form they may be either tubular or saccular and, when the central cavity, or the duct, is branched or divided the gland is said to be compound. There are consequently compound tubular and compound saccular (or racemose) glands. The secretory cells line the subdivisions of a tubular gland and the ultimate saccules, or acini, of a saccular gland. These glands are developed as involutions of the surface upon which they open and their epithelium is continuous with that of this surface. In the majority of cases the glands are derived from the integument and are of ectodermal origin: the glandular cells of the mid-intestine, however, are formed from the endoderm, and certain glands associated with the reproductive system are stated to be derived from the mesoderm.

Histologically a gland is composed of a layer of secretory epithelial cells which are provided with large and sometimes branched nuclei. Externally these cells are bounded by a membrana propria of connective tissue: internally they usually secrete a chitinous lining. In some cases the secretion of each gland cell is discharged through a minute intracellular ducteole which communicates with the lumen of the gland (Fig. 149).

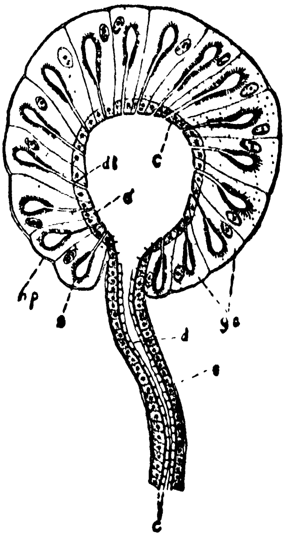

Fig. 149.—Semi-diagrammatic Section of an Acinus of the Pygidial Gland of a Carabid (*Pterostichus*).

c, chitinous lining; *d*, lumen of duct; *dt*, ducteole; *e*, epithelial lining of duct and *e* of acinus; *gc*, gland cells; *mp*, membrana propria; *s*, striated zone. Based on Dierckx, *La Cellule*, 16.

The principal types of glands are dealt with under the following headings.

Wax Glands (Fig. 150).—Glands which secrete wax are more especially characteristic of Homoptera where they are uni- or pluricellular structures distributed in various parts of the integument. They are particularly evident in the Coccidæ among which insects they retain their simple character. The wax is secreted in the form of a powdery covering, as a clothing of threads, or as thin lamellæ. Chinese white wax, which was formerly a commercial product, is secreted by the Coccid *Ericerus pe-la*. Wax glands are also frequent among Aphididæ and, in *Erisoma lanigera*, the wax is exuded both in a powdery and a filamentous condition. In the latter case it is discharged through plates composed of a ring or an aggregation of several large cells, each cell containing a central excavation, or wax chamber, within which the secretion accumulates (Fig. 150c). In the Fulgorid *Phromnia marginella* Bugnion and Popoff (1907) have shown that the dense clothing of waxy filaments which covers the nymphs is secreted by groups of unicellular glands composed of greatly elongated hypodermal cells (Fig. 150e). Overlying each group of cells is a chitinous plate studded with small pores which are the openings of the

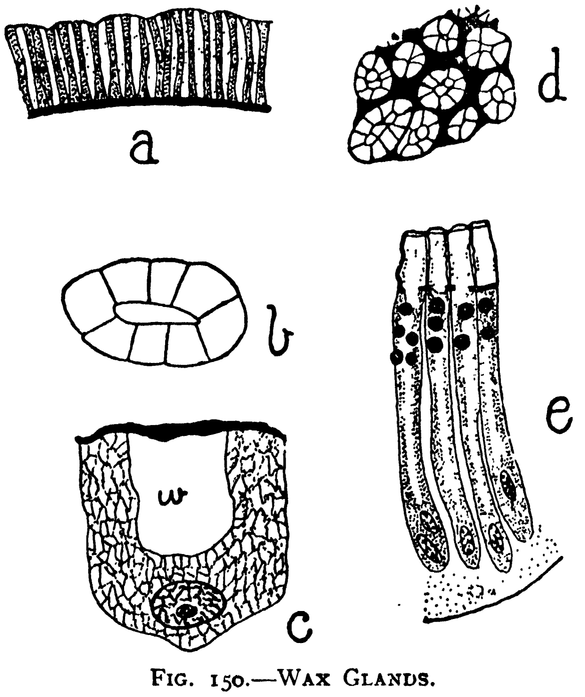

Fig. 150.—Wax Glands.

a, Section of a portion of a wax plate of a worker hive bee with gland cells (*after* Dreyling). *b*, Surface view of a wax plate of *Eriosoma lanigera* (apterous vivip. female). *c*, Section of a wax cell of the same showing wax chamber *w* (*after* Baker). *d*, Surface view of a portion of a wax plate of *Phromnia marginella*. *e*, Wax cells of the latter seen in section. *After* Bugnion and Popoff.

separate gland cells. The larvæ of some Coccinellidæ and of a species of *Selandria* (Tenthredinidæ) are invested with a mass of flocculent material believed to be of wax. The wax glands of the hive bee are alluded to under Hymenoptera (vide Dreyling, 1903–05).

Lac Glands.—Lac is secreted by certain Coccidæ and, in particular, by *Tachardia lacca*, *Gascardia madagascarensis* and by some species of *Coccus*. The first mentioned insect yields the lac of commerce which is a resinous substance produced in large quantities by the female insect as a protective covering. The lac is a product of gland cells distributed in the integument. Chemically it consists very largely of resin together with colouring matter, wax, proteids and small amounts of other substances. It is noteworthy that *Tachardia lacca* flourishes best on trees containing gums or resins, or which are rich in certain kinds of latex, and the food-plant influences the colour and quantity of the lac produced (vide Imms and Chatterjee, 1915).

Exuvial Glands.—In some insects there are specially enlarged hypodermal cells which secrete a fluid that facilitates the process of ecdysis (vide p. 194), such cells being known as exuvial glands. In the larva of *Bombyx mori* Verson and Bisson describe 15 pairs of unicellular glands of this kind of which there are two pairs in each thoracic segment, a pair on each abdominal segment from the 1st to the 7th, and two pairs on the 8th segment. In addition to other lepidopterous larvæ Plotnikov (1904) has found exuvial glands in larval Coleoptera, Tenthredinidæ and Chrysopidæ: they have also been described by Philiptschenko (1907) in Collembola.

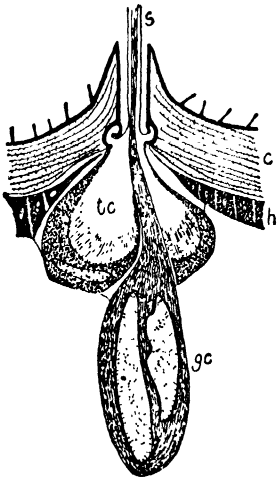

FIG. 151.—SECTION OF THE INTEGUMENT AND A GLANDULAR SETA OF THE LARVA OF *ARCTIA CAIA*.

c, cuticle; *gc*, gland cell; *h*, hypodermis; *s*, seta; *tc*, trichogenous cell. *After* Holmgren, *Ent. Tidsk.*, 1896.

Glands Associated with the Cuticular Appendages.—Under this category are various glands associated with specialized setæ or scales and their secretions exhibit urticating, alluring, or adhesive properties.

The urticating setæ of many lepidopterous larvæ are often grouped together on tubercles or processes of the body-wall. Each seta is commonly provided with a unicellular gland at its base, in addition to the usual trichogenous cell (Fig. 151): in some species (e.g. *Lagoa crispata*) there is a group of gland cells associated with each seta. The setæ are sharp and brittle and their cavities are filled with an urticating secretion. When a larva is handled such setæ are readily fractured, and their contained secretion often produces a cutaneous irritation, not unlike that caused by nettles.

On the wings of many male Lepidoptera there are peculiarly shaped scales known as *androconia* which are either distributed among the ordinary scales, or located in restricted patches. The characteristic odours of certain male butterflies appear to be produced by gland cells situated at the bases of the androconia, the latter functioning as organs for the outlet and dissemination of the secretion. The odours are believed to be of an alluring nature attractive to the opposite sex. Groups of odoriferous gland cells are often present in various other situations where they are associated with tufts of setæ or scales (Illig, 1902). Thus, in the males of *Hepialus hectus* (Fig. 152) the hind tibiæ are curiously swollen and bear patches of long clavate or cylindrical scales whose bases are connected with large gland cells (Deegener, 1902). In other male Lepidoptera they are either present at the base of the abdomen (*Acherontia atropos*, *Sphinx ligustri*, etc.) or at the apex of that region (Danainæ). Freiling (1909) has described odoriferous scales on the wings of both sexes of *Adopæa lineola* and *Acipitilia pentadactyla*: tufts of specialized scales or hairs in association with the genitalia in the females of *Gonepteryx rhamni*, *Stilpnotia salicis* and *Thaumatopæa pinivora*: and lateral saccules between the 8th and 9th abdominal segments in *Bombyx mori* (female).

Adhesive secretions are associated with the tenent hairs of Collembola, and the hairs clothing the ventral aspect of the tarsi, pulvilli, and arolia of many insects (Figs. 22, and 24, B), which enable them to walk up vertical surfaces, and on the undersides of various objects (vide Dewitz, 1884, 1885).

The aromatic secretions of various symphiline Coleoptera, living in the nests of ants or termites, are produced by dermal glands situated at the bases of tufts of hairs located in various regions of the integument.

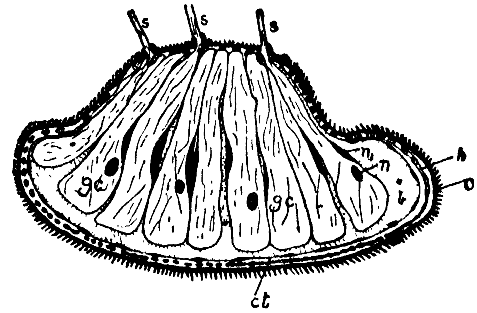

FIG. 152.—TRANSVERSE SECTION OF THE DISTAL PART OF THE HIND TIBIA OF *HEPIALUS HECTUS* (MALE).

b, blood space; *c*, cuticle; *ct*, connective-tissue sheath; *gc*, gland cells; *h*, hypodermis; *n*, central, n_1, peripheral nuclei of gland cell; *s*, scent scale. *After* Deegener, 1902.

General Segmental Glands.—In some larval insects metameric cutaneous glands are present on all or most of the segments of the thorax and abdomen (Figs. 147, 148). Among Tipulidæ they are well exhibited in the larva of *Gnophomyia* where there is a dorsal and ventral pair of simple saccular glands in each trunk segment: in several other genera these glands are simple cell aggregates whose secretion is discharged by means of intracellular ductules through a common pore (vide Keilin, 1913). In the larva of *Ocypus olens* Georgevitsch (1898) has described a pair of branched tubular glands in the head, and in each trunk segment, above the spiracles. A pair of dorsal glands is present in each segment of the larva of *Melasoma populi* (Berlese) and *Telephorus lituratus* (Payne): segmental glands also occur in certain larval Tenthredinidæ. The function of these organs is obscure. In Tipulid larvæ living in dry dead wood, they probably serve to keep the integument moist: in those living in mud, etc., they serve to protect the organism against asphyxiation when submerged. In coleopterous larvæ, and those of the Tenthredinidæ, they are stated to render the insects distasteful to their enemies.

Mandibular Glands.—Glands opening near the articulations of the mandibles are present in most lepidopterous larvæ, and in some species they are of large size (Fig. 153): they function as salivary glands, the true salivary glands being devoted to the secretion of silk. In the larva of *Sciara* they attain a great development and extend nearly the whole length of the body. Mandibular glands are also present in the hive bee and other adult Hymenoptera.

Maxillary Glands.—Glands belonging to the maxillary segment are sometimes present. They are found for example in Collembola, Protura in the larvæ of Neuroptera Planipennia and of certain Trichoptera.

Labial Glands.—These organs are commonly known as salivary glands which are paired structures, generally situated in the thorax, on either side of the fore-intestine. Their ducts combine to form a median salivary duct which opens on the labium, usually near the base of the hypopharynx. In many insects the ducts of the salivary glands possess tænidia in their chitinous lining, and bear a close resemblance to tracheæ. Although these glands appear to be often wanting in Coleoptera, they are present in the majority of insects and assume a great variety of form and structure. Among Orthoptera they are commonly very large and composed of a number of lobes, each lobe consisting of groups of glandular acini: a salivary reservoir is also present in relation with each gland (Fig. 154). In Hemiptera the salivary glands are differentiated to form two or three pairs, all of which discharge into the median salivary duct. In adult Lepidoptera the salivary glands form filamentous tubes. Among the majority of Diptera they are likewise tubular organs which, in the Muscidæ, may considerably exceed the total length of the body. Among Hymenoptera salivary glands are extremely well developed and assume great complexity. In the hive bee the true salivary glands consist of two pairs of racemose organs, one pair being cephalic and the other thoracic in position, and their four ducts unite to form a common canal. Under the category of salivary glands are also included the lateral and ventral pharyngeal glands and two pairs of mandibular glands found in this same insect.

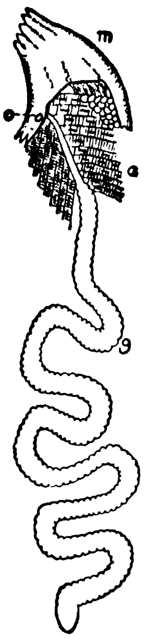

FIG. 153.—RIGHT MANDIBULAR GLAND (*g*) OF THE LARVA OF *ACHERONTIA ATROPOS*.

m, mandible and its adductor muscle *a*; *o*, external aperture of gland. *After* Bordas, *Ann. Sci. Nat. Zool.*, 1910.

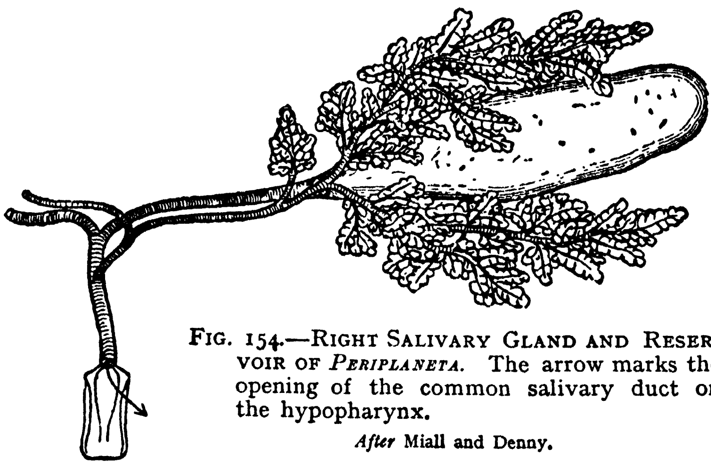

FIG. 154.—RIGHT SALIVARY GLAND AND RESERVOIR OF *PERIPLANETA*. The arrow marks the opening of the common salivary duct on the hypopharynx.

After Miall and Denny.

Comparatively little is known relative to the functions of the salivary glands. In some insects they have the property of converting starchy matter into assimilable glucose. In many blood-sucking insects the saliva possesses poisonous or irritant properties and, in some Diptera, Cornwall and Patton (1914) have detected a powerful anticoagulin. The exact means by which the frequent local irritation of the skin of the host is produced is still in doubt In certain

Capsidæ Smith (1920) has shown that the saliva has a violently toxic action upon plant tissues.

Silk Glands.—In lepidopterous and trichopterous larvæ the labial glands are transformed into organs for producing the silk utilized in the formation of the larval shelters and cocoons. The silk glands are cylindrical tubular organs of exceedingly variable length with characteristically branched nuclei (Fig. 155). The formation of silk has attracted the attention of a number of workers whose conclusions are summarized by Tanaka (1911). The silk is secreted in the form of a filament composed of fibroin, which is coated with a glutinous substance, sericin, formed by the transformation of the outer layer of the fibroin when the latter is oxidized and combined with molecules of water. In the larvæ of the Carabid *Lebia scapularis*, and of the Neuroptera Planipennia, silk is produced as a secretion of the Malpighian tubes: among Embioptera it is secreted by dermal glands situated in the anterior tarsi.

The Frontal Gland.— This is a median unpaired gland, peculiar to termites, and situated beneath the dorsal integument of the head, where it frequently opens by means of a frontal pore.

Thoracic Glands.—Dorsal thoracic glands are represented by the osmeteria of larval Papilionidæ, which are eversible repugnatorial organs, and the metanotal gland of the male *Œcanthus* which has an alluring function attractive to the female. Ventral thoracic glands are exemplified by the prothoracic glands of various lepidopterous larvæ, the odoriferous sternal glands of many Heteroptera, and Gilson's glands of larval Trichoptera. These and other thoracic glands are further alluded to in the chapters dealing with the orders concerned.

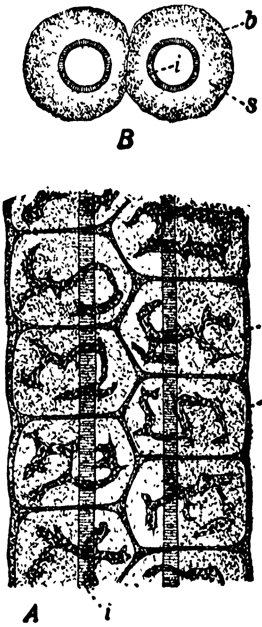

FIG. 155.—SECTIONS OF SILK GLAND OF THE LARVA OF *BOMBYX MORI*.

A, longitudinal; B, radial. *b*, basement membrane; *i*, chitinous intima; *s*, gland cell with branched nucleus. From Folsom *after* Helm.

Abdominal Glands.—Under the category of abdominal glands are the repugnatorial glands of many insects. Among the Blattidæ they are frequently pouch-like invaginations of either the sterna or terga. In the nymphs of many Heteroptera they open on to the terga of the anterior segments, and in *Cimex* they are present in the adult. Among Coleoptera, pygidial glands which open near the anus are frequent, particularly in the Adephaga. They are often of complex structure and their secretion has pungent or corrosive properties. Among lepidopterous larvæ eversible repugnatorial glands are present on the 6th and 7th segments in the Lymantriidæ and permanently everted lateral segmental glands occur in the Megalopygidæ. Dorsal eversible glands are present in many larval Lycænidæ and yield a secretion attractive to ants.

Glands Associated with the Reproductive System—These include the colleterial glands of the female and the accessory glands of the male (vide pp. 156, 160).

Poison Glands.—These organs are peculiar to Hymenoptera, where they are associated with the ovipositor or sting.

Literature on the Glands

The literature on the glands of insects is very extensive and only a relatively small number of the references are quoted below. Further literature is given under the various orders of insects and more extensive bibliographies will be found in the textbooks of Packard, Berlese, and Schröder.

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THE REPRODUCTIVE SYSTEM

THE form and structure of the reproductive organs present a very wide range of variation in different insects. In their embryonic condition they are at first essentially similar in the male and female, becoming differentiated later in development. Among the more primitive orders (Fig. 156) much of this similarity is still evident but an increasing divergence in structure becomes noticeable in the higher groups. The paired gonoducts, leading from the ovaries or testes as the case may be, are of mesodermal origin and in a few insects they open directly to the exterior by separate apertures. This archaic condition is exhibited among Ephemeroptera as well as in the immature *Lepisma* and in the males of the earwig *Labidura*: in the latter insect the ædeagus (vide p. 256) is also double. In other Dermaptera one gonoduct atrophies or only a rudiment of it persists. Among the vast majority of insects the gonoducts do not open directly to the exterior but join a median passage formed as a chitin-lined invagination of the ventral body-wall. In the Thysanura, Plecoptera and Odonata this passage is little more than a deep cup-like pit: in most other orders it becomes extended inwards in the form of a tube and in this manner the vagina in the female and ejaculatory duct in the male are developed. In some Coleoptera the median ectodermal passage gives off paired distal outgrowths and the two tubes, thus formed, unite with the paired mesodermal ducts already mentioned.

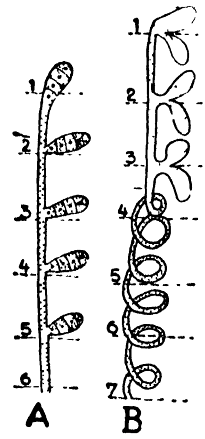

FIG. 156.—GONADS OF A YOUNG *LEPISMA* (MESODERMAL PORTIONS ONLY).

A, female; *B*, male. The numerals refer to the abdominal segments. Adapted from Grassi, 1887.

The genital aperture is usually situated on the 8th or 9th abdominal sternum or between the 8th and 9th or 9th and 10th sterna: its segmental position, however, frequently differs in the two sexes of the same species and in different orders.

The sexual organs, and their counterparts in the male and female, may be tabulated as below.

MALE REPRODUCTIVE ORGANS	FEMALE REPRODUCTIVE ORGANS
1. Paired testes composed of follicles (testicular tubes)	Paired ovaries composed of ovarioles (ovarian tubes)
2. Paired vasa deferentia	Paired oviducts
3. Vesiculæ seminales	Egg-calyces
4. Median ejaculatory duct	Median vagina
5. Accessory glands:	Accessory glands:
(*a*) Mesadenia	(*a*) ——
(*b*) Ectadenia	(*b*) Colleterial glands
6. ——	Spermatheca
	Bursa copulatrix
7. Genitalia	Ovipositor

The sexes of insects are separate or it is only very rarely that hermaphroditism is present as a normal condition (vide p. 166). Another phenomenon, known as *gynandromorphism,* is often confused with hermaphroditism and occurs abnormally in various insects, especially Lepidoptera, where several thousands of examples have been recorded. Gynandromorphs are sex mosaics which exhibit on one side of the body all the characters, shape and colour of one sex and on the other side those of the opposite sex (Fig. 157). The male and female parts lie adjacent and equivalent to each other and are present simultaneously during development. More rarely gynandromorphs are antero-posterior in type, or even a more complex type of mosaic may result. Other tetralogical types of individuals known as *intersexes* also occur which exhibit various blending of the male and female characters. Each individual develops initially as a male (or female) up to a certain time point. A change over then occurs and the development continues as an individual of the opposite sex. The earlier the change over takes place the more pronounced is the degree of intersexuality produced. In a few words, a gynandromorph is a sex mosaic in space and an intersex is a sex mosaic in time. For a discussion of the causal factors involved vide Goldschmidt (1923).

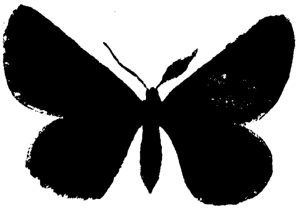

FIG. 157.—GYNANDROMORPH OF *BUPALIS PINIARIA*: RIGHT SIDE MALE, LEFT SIDE FEMALE.

After Dziurzynski, *Berlin Ent. Zeits* 1912.

1. The Male Reproductive Organs (Figs. 158–160)

The Testes.—The testes in most Apterygota closely resemble the ovaries in form and size but in the majority of insects they are much smaller than the organs of the female of the same species. They are variably situated in relation to the alimentary canal and in some cases they lie above the latter, in others they are placed at the sides of the gut or wholly ventral to it. The testes are maintained in position by the surrounding fat-body and tracheæ and, unlike the ovaries, there are no suspensory filaments or the latter are only very slightly developed. As a general rule, each testis is a more or less ovoid body composed of a variable number of follicles or lobes which also present almost innumerable variations in form and arrangement among different insects. In *Lepisma* there are three or four bi-lobed follicles which exhibit a segmental disposition but in most Apterygota each testis is a simple sac or greatly enlarged follicle. Among Neuroptera and Diptera the testes are small and unifollicular : in *Pediculus* and *Phthirius* they are bifollicular, and in the Orthoptera the follicles are exceedingly numerous. They may be short and globular as in *Periplaneta* and *Tetrix,* or elongate and tubular as in *Œdipoda.* In the Anoplura, also in *Melolontha* and certain other Coleoptera, each follicle is connected with the vas deferens by a slender tube or *vas efferens.* In many insects the peritoneal investment of the follicles is developed to the extent of enveloping the testis as a whole in a common coat or *scrotum* which is frequently pigmented. Among the majority of Lepidoptera, also in *Gryllotalpa* and certain Hymenoptera, the testes are in close contact along the median line and are enclosed in a single scrotum.

The Structure of a Testicular Follicle.—The testicular follicles are lined with a layer of epithelium, whose cells rest externally upon a basement membrane, outside of which there is a peritoneal coat of connective tissue. Each follicle is divided into a series of zones characterized by the presence of the sex cells in different stages of development, corresponding to the successive generations of these cells. These zones are as follows—

(1) The *germarium* is the region containing the primordial germ cells or spermatogonia which undergo multiplication.

(2) The *zone of growth* is where the spermatogonia increase in size and develop into spermatocytes of the first and second orders.

(3) The *zone of division and reduction* where the spermatocytes undergo mitosis and give rise to spermatids.

(4) The *zone of transformation* where the spermatids become transformed into spermatozoa.

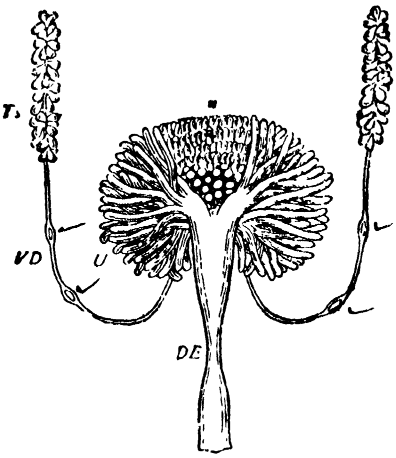

FIG. 158.—MALE REPRODUCTIVE ORGANS OF *PERIPLANETA*, VENTRAL VIEW.

Ts, testis; *VD*, vas deferens; *u*, *U*, accessory glands; *DE*, ejaculatory duct. *After* Miall and Denny.

In addition to the sex cells there are found in Lepidoptera, and some other insects, certain larger elements known as Verson's cells. The function of these cells has received diverse interpretations, some authorities regarding them as contributing to the nutrition of the germ cells.

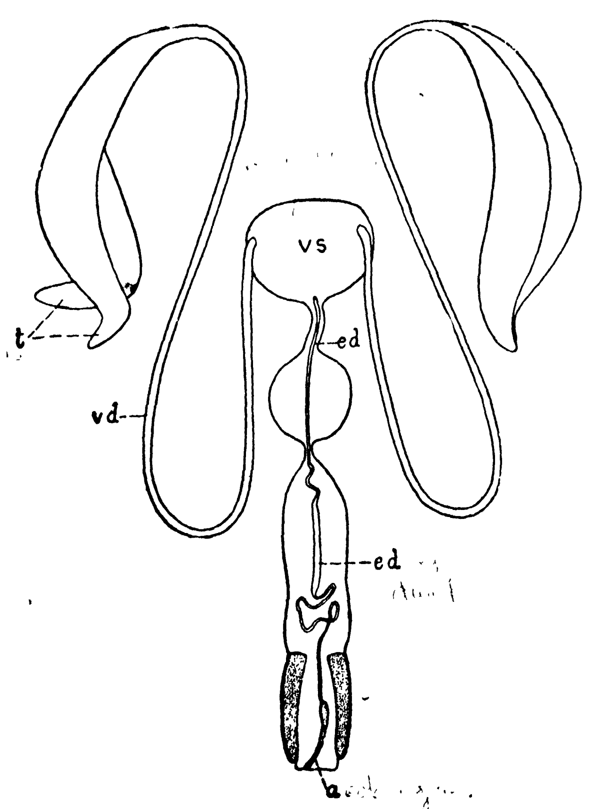

FIG. 159.—MALE REPRODUCTIVE ORGANS OF *FORFICULA AURICULARIA*.

t, testis; *vd*, vas deferens; *vs*, vesicula seminalis; *ed*, ejaculatory duct; *a*, ædeagus.

The Genital Ducts.—The *vasa deferentia* are the paired canals leading from the testes and are wholly mesodermal in origin. They vary greatly in length and, in the majority of insects, each vas deferens becomes enlarged along its course to form a sac or *vesicula seminalis* in which the spermatozoa congregate: in some of the Diptera the vasa deferentia open into a common vesicula seminalis. Histologically the vas deferens consists of an outer peritoneal coat, a middle ~~coat of muscle fibres, and~~ an ~~inner coat of epithelial~~ cells. Posteriorly, the vasa deferentia unite to form a short common canal which is continuous with a median ectodermal tube or ejaculatory duct. The latter is provided with

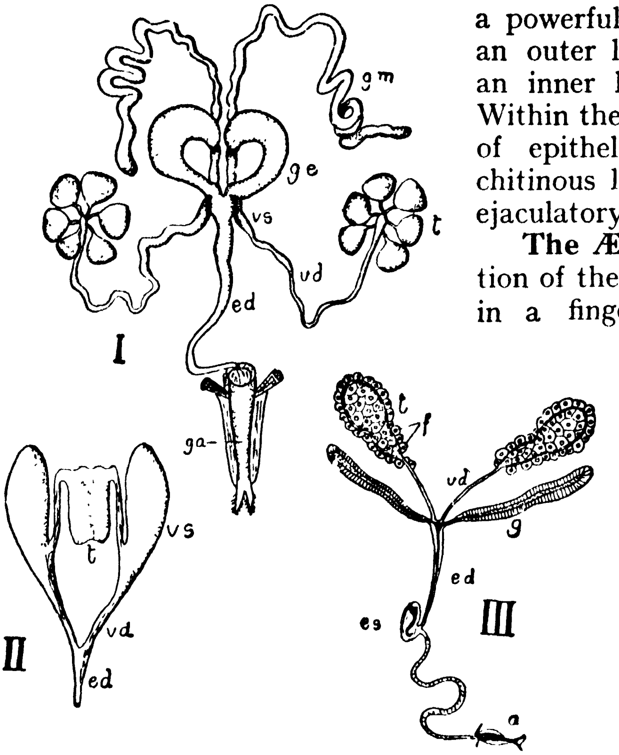

FIG. 160.—MALE REPRODUCTIVE ORGANS. I, *Tenebrio obscurus*, *after* Bordas, 1900. II, *Sphecodes fuscipennis*, *after* Bordas, 1895. III, *Calliphora*, *after* Lowne.

a, ædeagus; *ed*, ejaculatory duct; *es*, ejaculatory sac; *f*, fat cells; *ga*, gonapophyses; *g*, accessory gland; *ge*, do., ectadenes; *gm*, do., mesadenes; *t*, testis; *vd*, vas deferens; *vs*, vesicula seminalis.

a powerful muscular coat consisting of an outer layer of circular fibres and an inner layer of longitudinal fibres. Within the muscle layers is a stratum of epithelial cells which secrete a chitinous lining to the lumen of the ejaculatory duct.

The Ædeagus.—The terminal section of the ejaculatory duct is enclosed in a finger-like evagination of the ventral body-wall which forms the male intromittent organ or *ædeagus* (often incorrectly termed the penis). The structure of the ædeagus (Fig. 161) has been chiefly studied by Sharp and Muir in Coleoptera where it is developed as a medium tubular evagination of the membrane between the 9th and 10th sterna. It is divisible into a proximal portion (tegmen), which unites it to the abdomen, and a distal portion (median lobe) which corresponds to a penis. The latter region is telescoped or retracted within the proximal portion when at rest. Both portions are usually strengthened with chitinous sclerites. The region of the ædeagus, which completely enters the vagina of the female during coitus, is the enlarged terminal portion of the ejaculatory duct (internal sac), which becomes everted in the process (Fig. *A*). At its apex is situated the genital aperture and around the latter there is frequently an armature of denticles and papillæ.

The Accessory Glands.—From one to three pairs of accessory glands are usually present in relation with the genital ducts (vide Escherich 1894: Blatter 1897). They are tubular or sac-like in form, but very little information exists with regard to their functions. In most cases their

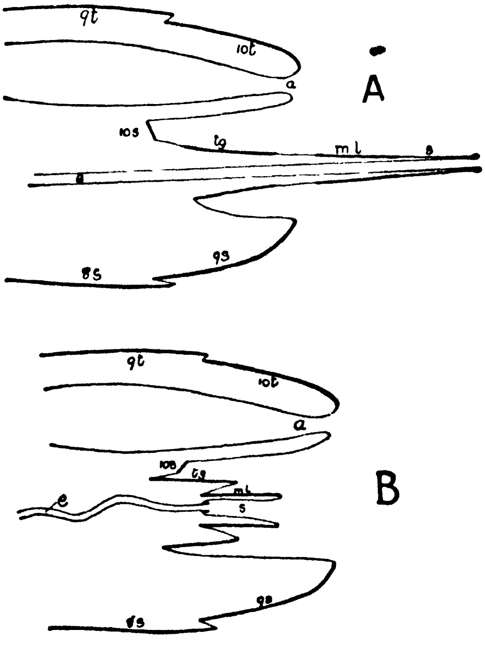

FIG. 161.—DIAGRAM OF THE ÆDEAGUS OF A BEETLE.

A, extended; B, retracted. *a*, anus; *e*, ejaculatory duct; *ml*, median lobe; *tg*, tegmen; *s*, internal sac; 8*s*–10*s*, sterna; 8*t*–10*t*, terga. Based on Sharp and Muir, 1912.

secretions mix with the spermatozoa and in some insects they are directly concerned with the formation of the spermatophores. According to Beauregard the secretion of the 3rd pair of accessory glands in *Lytta vesicatoria* is extremely rich in cantharidin. Escherich divides the accessory glands into two categories : (1) *mesadenia*, or those derived from the mesoderm, and formed as evaginations of the vasa deferentia : and (2) *ectadenia*, or those of ectodermal origin, and formed as evaginations of the ejaculatory duct (Fig. 160). This classification may be adopted as a convenient one, but due reservation needs to be made on account of the paucity of knowledge concerning the development of these organs. Escherich's observations relate to Coleoptera and among these insects ectadenia are generally present. In the Adephaga they constitute the only pair of accessory glands while among the Polyphaga one or more pairs of mesadenia are also present. Among Orthoptera the accessory glands are very greatly developed, forming dense bunches of tubuli which, in *Periplaneta*, form the " mushroom-shaped gland " of Huxley. The accessory glands are wanting in some insects, including the Apterygota, and *Musca*, *Tabanus*, etc., among Diptera.

2. The Female Reproductive Organs (Figs. 162–164)

The Ovaries.—The ovaries are typically more or less compact bodies lying in the body-cavity of the abdomen on either side of the alimentary canal. Each organ is composed of a variable number of separate egg-tubes or *ovarioles* which open into the oviduct. The primitive number of ovarioles composing an ovary is uncertain and probably does not exceed eight, the latter number being retained in *Periplaneta*, for example, among Orthoptera. In some Thysanura (*Japyx*, *Campodea* and *Lepisma*) there are 5–7 ovarioles on each side which open one behind the other in metameric succession into an elongate oviduct. In other insects this metameric disposition has become lost owing to the shortening of the oviducts. Specialization either by the reduction or the multiplication of the ovarioles is extremely frequent. In insects which produce a small number of relatively large eggs such as the viviparous Diptera *Glossina* and *Termitoxenia* there is a single ovariole to each ovary. In certain of the Aphididæ, in the sexual female there is a single ovary with one ovariole, the other ovary having atrophied. Two ovarioles are present in each ovary of *Melophagus*, *Hippobosca*, and certain Coleoptera and Hymenoptera : among Lepidoptera there are commonly four. Examples of specialization by multiplication are much more frequent. Thus in *Calliphora* and *Hypoderma* there are 100 or more ovarioles to an ovary ; in some ants there are over 200 ; in *Melöe* they are even more numerous while the maximum number is attained in the Isoptera where among species of *Termes* it exceeds 2,400. In a few appar-

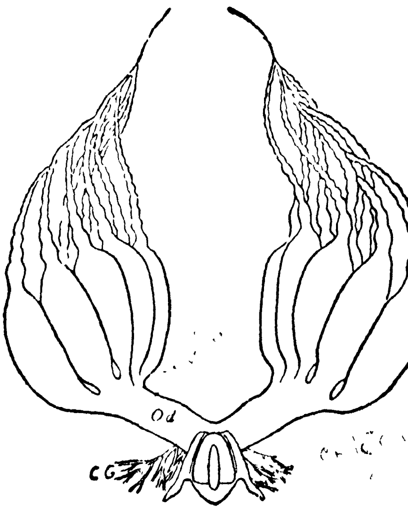

FIG. 162.—FEMALE REPRODUCTIVE ORGANS OF *PERIPLANETA*.

Od, oviduct ; *CG*, colleterial gland. *After* Miall and Denny.

ently anomalous instances ovarioles are wanting and the ovaries are more or less sac-like without any serial arrangement of the developing eggs. Such ovaries are well exhibited among Collembola. In *Chironomus*, *Anopheles* and some Braconidæ (*Aphidius*) although there is an evident differentiation into follicles ovarioles are wanting: this is a secondary and highly modified condition (vide Henneguy).

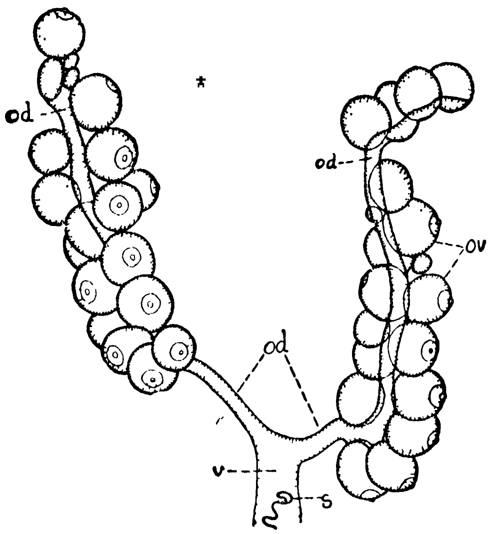

FIG. 163.—FEMALE REPRODUCTIVE ORGANS OF *FORFICULA AURICULARIA*.

od, oviduct; *ov*, ovarioles; *v*, vagina; *s*, spermatheca.

The Ovarioles.—A typical ovariole is an elongate tube in which the developing eggs are disposed one behind the other in a single chain, the oldest oocytes being situated nearest the union with the oviduct. The wall of an ovariole is a delicate transparent membrane: its inner coat is a layer of epithelium whose cells rest upon a basement membrane or tunica propria: outside the latter is a peritoneal coat of connective tissue which, in many insects, contains a reticulum of muscle fibres.

Three zones or regions are recognizable in an ovariole (Fig. 165)—(1) The *terminal filament.* This is the slender thread-like apical prolongation of the peritoneal layer. The filaments of the ovarioles of one ovary combine to form a common thread which unites with that from the ovary of the opposite side to form a median ligament. The latter aids in maintaining the ovaries in position and is attached either to the body-wall, the fat-body or to the pericardial diaphragm. In some insects the ovarian ligament is wanting and the filaments end free in the body-cavity. (2) The *germarium.* This forms the apex of an ovariole, below the terminal filament, and consists of a mass of cells from which are differentiated the primordial germ cells and, in many insects, the nutritive cells also. (3) The *vitellarium.* The vitellarium constitutes the

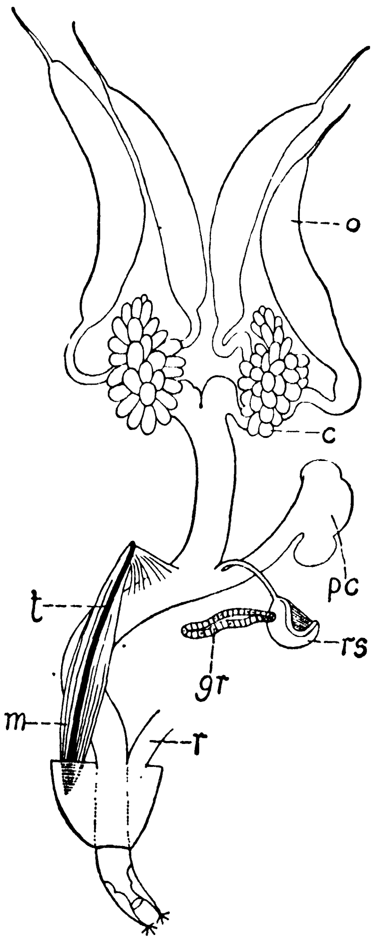

FIG. 164.–FEMALE REPRODUCTIVE SYSTEM OF *ANTHONOMUS POMORUM*.

c, egg-calyx; *m*, vaginal muscle and spiculum *t*; *o*, ovariole; *pc*, bursa copulatrix; *r*, rectum; *rs*, receptaculum seminis and gland *gr*. *After* Henneguy, "Les Insectes."

major portion of an ovariole and contains the developing eggs and the nutritive cells when present. The epithelial layer of the wall of the vitellarium grows inwards in such a manner as to enclose each oocyte in a definite sac or follicle. The cells of the follicle secrete the chorion of

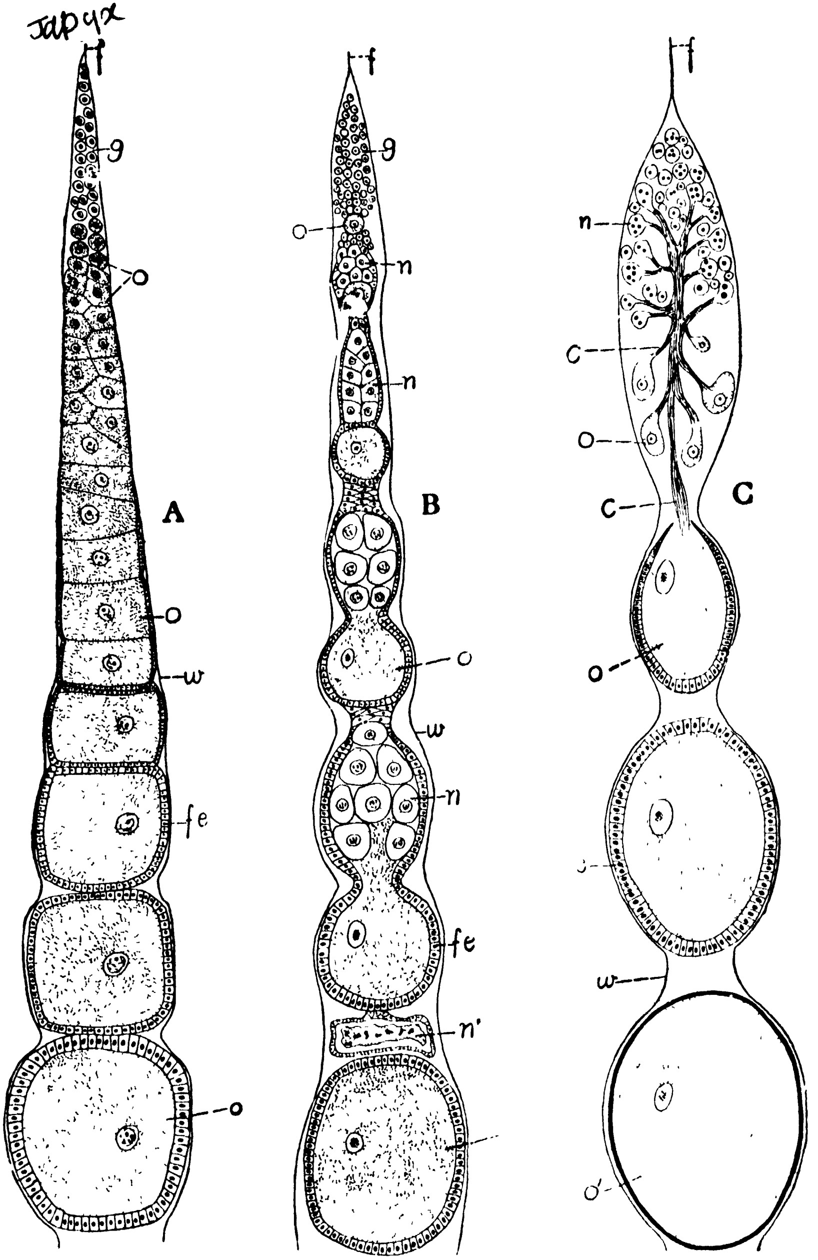

FIG. 165.—SCHEMATIC FIGURES OF THREE TYPES OF OVARIOLES.

A, panoistic. B, polytrophic. C, acrotrophic. *f*, terminal filament; *g*, germarium; *o*, oocytes; *o'*, mature oocyte with chorion; *n*, nutritive cells; *n'*, remains of same; *w*, wall of ovariole; *fe*, follicular epithelium; *c*, cord joining nutritive cells with oocyte.

the egg and in some cases serve to nourish the oocytes. Three principal types of ovarioles are recognized and are based upon the presence or absence of nutritive (or vitellogenous) cells and on the location of these cells when present (Fig. 165).

(*a*) The *panoistic type*.—Nutritive cells are wanting. This type of ovariole is primitive and is found in *Japyx*, the Orthoptera, Isoptera, Odonata and Aphaniptera.

(*b*) The *polytrophic type*.—Nutritive cells are present and alternate with the oocytes. In many cases (Neuroptera, Coleoptera-Adephaga and Hymenoptera) the nutritive cells are grouped together so as to lie in chambers, each chamber being separated from that containing an oocyte by a well-marked constriction; in others (Lepidoptera, Diptera) these constrictions are wanting.

(*c*) The *acrotrophic type*.—Nutritive cells are present and situated at the apices of the ovarioles (Coleoptera-Polyphaga and Hemiptera). In certain Heteroptera the nutritive cells are connected with the oocytes by means of protoplasmic cords.

Types (*b*) and (*c*) are often grouped as one type—*meroistic*, which is characterized by the presence of nutritive cells.

The Genital Ducts.—The *oviducts* are the paired canals leading from the ovaries and are derived from the mesoderm of the hinder extremities of the embryonic gonads. The two oviducts combine to form a *common oviduct* and the latter is continuous posteriorly with a somewhat wider passage or *vagina*: in many insects however there is no external distinction between the two regions but the vagina differs morphologically in that it is an invagination of the body wall. In some Coleoptera, especially Rhynchophora, so-called *egg-calyces* or corpora lutea develop as outgrowths of the oviducts (Fig. 164). They do not attain their full development until after fertilization and their function in relation to the eggs is obscure. According to Buchner they are developed in connection with symbiotic microörganisms. In certain viviparous insects (*Glossina*, *Melophagus*, etc.) the vagina is greatly enlarged to form a chamber or *uterus* for the reception of the developing larva. Structurally the oviducts and vagina are composed of an epithelial layer whose cells secrete an inner lining: in the case of the vagina the lining is composed of chitin and is continuous with the cuticle of the body wall. The epithelial layer rests upon a basement membrane and outside the latter is a coat of powerful, and mainly circular muscle fibres.

The Spermatheca (*receptaculum seminis*).—This is a pouch or sac for the reception and storage of the spermatozoa. It varies greatly in form and usually opens by a duct (often reduced to a mere neck) into the dorsal wall of the vagina or into the bursa copulatrix. In many insects pairing only takes place once and, since the maturation of the eggs may extend over a prolonged period, the provision of a spermatheca allows for their fertilization from time to time. Although commonly ovoid or spherical in form, in some cases (certain Coleoptera) it is tubular, or even branched as in *Paederus*. As a rule the spermatheca is a single organ but in *Blaps*, *Phlebotomus* and *Dacus* there are two spermathecæ and in *Culex*, the Tabanidæ and most Calypteræ three. Since it is derived from the ectoderm the spermatheca is lined with cuticle which is sometimes darkly or brightly coloured. A stratum of columnar epithelium rests upon a basement membrane which is followed by a muscular coat. In some cases glandular cells are present in the wall of the spermatheca and in others a special *spermathecal gland* opens into the duct of the spermatheca, or near the aperture of the latter into the vagina.

The Colleterial Glands.—One or two pairs of accessory glands are present in most insects and open into the distal portion of the vagina. These are variously known as colleterial or sebific glands and are very large and important organs in many of the Orthoptera. In these insects they provide the material for the formation of the ootheca: in *Chironomus* they secrete a mucus-like substance which forms the gelatinous investment of the eggs, and in other cases they simply provide a cement-like secretion which serves to fasten the eggs down to the substratum upon which they are laid. The poison glands of Hymenoptera belong morphologically to the same category as the colleterial glands.

The Bursa Copulatrix.—The organ to which this name has been applied exists in several morphologically different forms. It is adapted to receive the penis and associated parts during copulation, the spermatozoa being discharged into it before entering the spermatheca. In *Periplaneta* the bursa is formed by the invagination of the body wall around the genital aperture and consequently receives the latter anteriorly. In Odonata the oviduct opens directly into a chamber which has been termed the burs and also functions as a spermatheca. In the honey-bee the enlarged posterior region of the vagina is known by the same name. In *Melanoplus* and the Lepidoptera the bursa has a distinct external opening separate from that of the vagina. In the first mentioned instance there is no connection between the two and the eggs, as they are extruded, pass across the opening of the bursa where they are fertilized. Among Lepidoptera a fine canal connects the bursa with the vagina. In Coleoptera the bursa is a pouch-like outgrowth of the vagina and in some species it receives the duct of the spermatheca.

3. The Sex Cells

The Spermatozoa.—The spermatozoa of insects exhibit the same essential structure that obtains with few exceptions in similar cells throughout the animal kingdom. A spermatozoon consists of a head largely made up of chromatin, a middle piece and a vibratile tail of variable and often complex structure (vide Ballowitz, 1890).

In some insects (Gryllidæ, Locustidæ, Odonata and certain Lepidoptera) the spermatozoa are transferred to the genital passage of the female in a common mass enclosed in a definite envelope, the whole being known as a *spermatophore.* In *Gryllus campestris* the spermatophore is a complex body about 4 mm. long, bearing crochets which ensure its retention within the female.

The Eggs.—When the egg of an insect is mature its protoplasm contains abundant yolk or vitellus which serves to nourish the developing embryo. This material is composed of globules of fat and protein which largely conceal the nucleus or germinal vesicle. The egg is invested by a delicate homogeneous *vitelline membrane* derived from the peripheral protoplasm of the cell. Outside this covering a hardened shell or chorion is secreted by the follicular epithelium. The chorion is generally composed of two laminæ, an exochorion and an endochorion, which are united by minute trabeculæ. In many endoparasitic Hymenoptera the chorion is thin and membranous, and capable of stretching to a considerable degree with the growth of the contained embryo. Among many viviparous insects it is either rudimentary or wanting. The chemical nature of the choron has been investigated by Verson with reference to the eggs of *Bombyx mori.* Unlike chitin it contains sulphur and upwards of 17 per cent. of nitrogen: at a temperature of 45° C. it dissolves in a few hours in a 3 per cent. solution of KOH.

In the greater number of insects the chorion exhibits some form of external sculpture: very commonly it is marked out into hexagonal areas which correspond with the overlying follicular cells. In the Lepidoptera the eggs of many species are conspicuously ribbed and in some Ephemeroptera they are covered with fine processes resembling pile. The form assumed by the eggs presents innumerable variations (Fig. 166): one of the commonest types is the elongate-ovoid and slightly curved egg prevalent among Orthoptera, and in many Diptera and aculeate Hymenoptera. Among Lepidoptera the eggs may be almost spherical, cake-like or somewhat cylindrical and flattened at one end: in many parasitic Hymenoptera there is a tubular prolongation or pedicel. In some insects an operculum is formed as a special differentiation of the chorion at the anterior extremity. This structure is uplifted at the time of eclosion of the contained insect and is well seen in the Embioptera, *Cimex* and other Heteroptera, and in the Anoplura. In the Œstridæ, the eggs are provided with flanges which enable them to grasp the hairs of the host upon which they are laid.

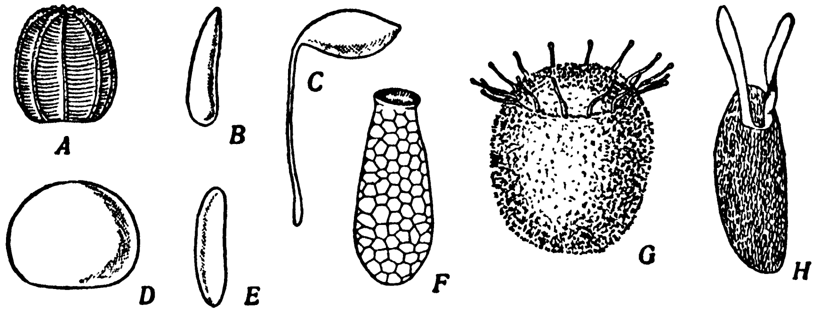

FIG. 166.—EGGS OF VARIOUS INSECTS.

A, butterfly, *Polygonia interrogationis*; B, *Musca domestica*; C, chalcid, *Bruchophagus funebris*; D, *Papilio triolus*; E, midge, *Dasyneura trifolii*; F, hemipteron, *Triphleps insidiosus*; G, hemipteron, *Podisus maculiventris*; H, *Drosophila ampelophila*. Greatly magnified. *After* Folsom, 1923.

Owing to the impenetrable nature of the chorion, and the fact that the latter is formed before the egg is fertilized, some provision is necessary to enable the spermatozoa to gain admittance. One or more specialized pores or canals known as *micropyles* are present for this purpose, and are usually situated at the anterior or cephalic pole of the egg. In *Phyllodromia* there are numerous micropyles which are comparatively simple, oblique, wide-mouthed canals. Among Lepidoptera the micropylar area is in the form of an elaborate sculptured plate. In *Nepa cinerea* it is provided with stalk-like processes, and in other Heteroptera it assumes a remarkable complexity of structure the significance of which is quite obscure.

4. Types of Reproduction

Ordinarily reproduction among insects is dependent upon the meeting of the two sexes and the fertilization of the ovum by the spermatozoon. Most insects are oviparous or, in other words, they lay eggs which hatch after deposition. Exceptions to the above generalizations, however, are somewhat numerous and are separately dealt with below.

Viviparity.—A certain number of insects produce either larvæ or nymphs instead of laying eggs and are said to be viviparous (vide Holmgren 1904: Keilin 1916). Viviparity is due to the fact that the eggs are retained within the body until the end of embryonic life and the contained insect has emerged. It is found in scattered instances among the Orthoptera, Dermaptera, Ephemeroptera, Lepidoptera and Coleoptera: in the Aphididæ and a number of the Diptera it is a regular feature. In the latter order of insects almost every transition is exhibited between species which lay a large number of small eggs from which the larvæ hatch before or just at the time of oviposition (many Tachinidæ), and such highly specialized forms as *Glossina* and *Melophagus*. In the two latter instances only a small number of eggs are produced and each larva passes its life in the uterus of the female where it is nourished by a special secretion. After extrusion it changes almost immediately into a pupa.

Among the Aphididæ viviparity is accompanied by parthenogenesis and in a few other insects it is associated with pædogenesis.

Parthenogenesis.—Parthenogenesis, or reproduction without the act of fertilization, exhibits a multiplicity of phases among insects that is unequalled in any other class of the animal kingdom (vide Doncaster 1914, 1920). In some species it is a comparatively rare phenomenon and only occurs sporadically. In others it is a constant and normal method of reproduction, or it may be cyclic alternating with sexual reproduction. It is convenient, therefore, to classify parthenogenesis under three headings.

1. SPORADIC.—Certain species of insects exhibit an occasional tendency to reproduce parthenogenetically although males are of regular occurrence. Such cases have been more frequently observed among Lepidoptera than in other orders and are more prevalent in some species than in others. Instances of this kind are well known in *Bombyx mori*, *Lymantria dispar*, *Lasiocampa quercus* and *Smerinthus populi*. Both males and females may be produced from the unfertilized eggs.

2. CONSTANT.—In most insects which reproduce parthenogenetically the process is either a constant one or takes place with such frequency that it is to be regarded as a normal phenomenon of the species concerned. In the social Hymenoptera males are regularly produced from the unfertilized eggs and females from those which are fertilized. This same fact has also been observed, but very little investigated, among the parasitic groups of that same order, notably in a number of genera of Chalcidoidea. In other cases males are either unknown, or very infrequent, and reproduction is consequently always or nearly always parthenogenetic. Examples of this kind are frequent among the Tenthredinidæ. Other cases are met with in the Cynipid *Rhodites rosæ*; in the Chalcids *Aphelinus mytilaspidis* and *Isosoma grandis*; and in certain Phasmidæ, Coccidæ, Aleyrodidæ, Psychidæ and in several of the Thysanoptera. The Tenthredinidæ, it may be mentioned, are remarkable in that among their members are found species that produce males only, females only, or both males and females by means of virgin eggs. Among the Aleyrodidæ the unfertilized females usually give rise only to males but in *Aleyrodes vaporariorum* there appears to be two races, the virgin females of one giving rise to males and of the other to females (Schrader, 1920): the fertilized females produce members of both sexes.

3. CYCLIC.—In other cases one or more agamic generations alternate with a sexual generation. This peculiarity is exhibited among the Cynipidæ, and the Aphididæ. In the former group the individuals of the two generations may be morphologically very different and produce very dissimilar galls. The spring generation consists of females which give rise to the summer generation comprising individuals of both sexes. Among the Aphididæ there is a regular sequence of parthenogenetic generations, accompanied by viviparity, in which females only are produced. Later in the year sexuales appear and the fertilized females lay eggs which hibernate and give rise to the asexual cycle of the following year.

Pædogenesis.—In a few instances larvæ or pupæ are capable of parthenogenetic reproduction and this process, which involves the production of young by the immature organism, is termed pædogenesis. The best known instance of the phenomenon occurs in the Cecidomyiid *Miastor* where it was first observed by Wagner in 1862. His remarkable discovery has since been confirmed by a number of observers, including Kahle (1908) and Hegner (1914), and more recently by Harris and by Gabritschevsky. The female fly contains only 4 or 5 very large eggs which attain nearly the full length of the abdomen. Each egg develops into a correspondingly large transparent larva which produces pædogenetically from about 7 to 30 daughter larvæ of similar characters to the parent. After devouring much of the tissues of the latter, the larvæ eat their way to the exterior and reproduce by a similar method on their own account. After the process has gone on for several generations of larvæ pupation takes place and male or female flies are produced. The latter, after fertilization, give rise to the pædogenetic cycle over again. In *Miastor americana* Felt, the ovaries lie on either side of the body of the larva in the 10th or 11th segment : each ovary contains typically 32 oocytes and is enclosed in a thin cellular envelope : as some of the oocytes fail to develop, usually 5–17 embryos are found in an individual larva (Hegner).

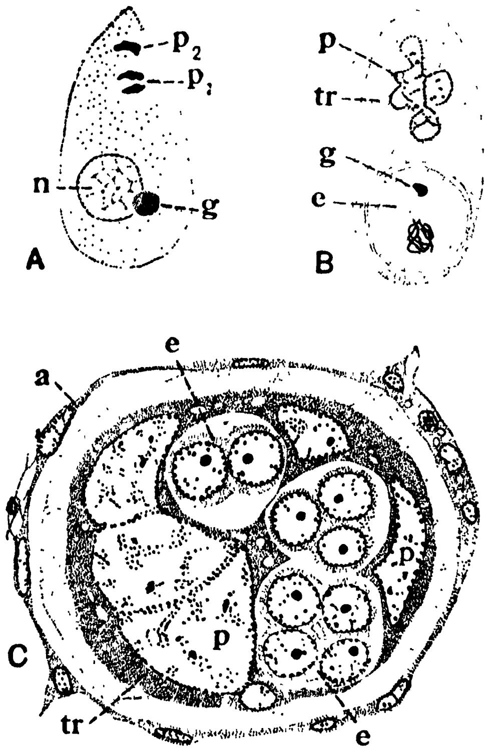

FIG. 167.—*ENCYRTUS FUSCICOLLIS*, POLYEMBRYONIC DEVELOPMENT.

A, egg with 1st and 2nd polar bodies p_1, p_2 ; *n*, oocyte nucleus. B, division of egg into embryonic area *e* and trophamnion *tr* with paranucleus *p* ; *g*, germ cell determinant. C, transverse section of polyembryonic mass ; *a*, adventitious sheath ; *e*, *e*, embryos. From Martin.

The studies of Harris (*Psyche*, 1923–24 ; *Biol. Bull.* 48, 1925) and of Gabritschevsky (*Bull. Soc. Ent. Fr.* 1928) show that the larvæ of both *Miastor* and *Oligarces* are trimorphic. They are divisible into (*a*) typical, white, pædogenetic larvæ without a sternal spatula ; (*b*) yellow, pædogenetic larvæ without a sternal spatula, and whose significance is obscure ; and (*c*) pupa-forming larvæ, with a sternal spatula, which develop directly into adult flies. It is noteworthy that environmental conditions influence the occurrence of these types and that only flies of one sex are derived from the same individual larva.

Pupal pædogenesis occurs in the Chironomid *Tanytarsus* where it was discovered by Grimm in 1870, whose observations have been extended by Zavrel. The pupæ, and also the ~~imagines~~ imagos very shortly after emergence, are capable of producing eggs from which larvæ duly emerge. Pædogenesis is also recorded by Barber in larvæ of the beetle *Micromalthus*.

Polyembryony.—Polyembryony is the production of two or more embryos from a single egg by gemmation. This process is only known in a few groups of animals and, among insects, it occurs in some parasitic Hymenoptera. It is most prevalent in the Chalcid family Encyrtidæ, but is also known in the Proctotrypoidea, Ichneumonoidea and Vespoidea. Since the fundamental discovery of polyembryony in *Ageniaspis* (*Encyrtus*) *fuscicollis*, a parasite of *Hyponomeuta*, by Marchal in 1904, a number of investigators have studied the process in different insects. Among the Chalcidoidea it has been recorded in species belonging to five genera whose hosts are Lepidoptera. In all cases the eggs of the parasites are laid in those of their hosts, which duly hatch into larvæ with the developing parasites in their bodies. The main features of polyembryonic development are very similar in different parasites (Fig. 167). The oocyte nucleus forms two polar bodies and the first of the latter may divide: subsequently the cytoplasm becomes differentiated into an embryonic area, around the nucleus, and a polar area associated with the polar bodies. The embryonic nuclei undergo division while the polar nuclei give rise to the paranucleus or nucleus of the trophamnion. The latter comes to surround the embryonic area while the egg, as a whole, soon becomes enclosed in an adventitious sheath formed from the surrounding host tissues. The trophamnion is believed to absorb food material from the host and act as the means of transferring such products to the embryos since the original egg is very deficient in yolk. The beginning of polyembryony is the division of the embryonic area into small groups of cells, or morulæ, which lie in cavities within the trophamnion. The whole egg increases in size, further morulæ are formed, while the trophamnion and adventitious sheath grow simultaneously as a complete double coat. The process goes on and results in a chain of embryos (Fig. 168), derived from the morulæ, which ultimately break away and become endoparasitic larvæ. The number of embryos which originate from a single egg is very variable: in *Copidosoma testaceipes* from about 163 to 191 are recorded (Patterson, Leiby) and in *Litomastix truncatellus* about 1,500 embryos are formed (Silvestri). In the latter species two types of larvæ result, i.e. those with gonads and asexual larvæ, but only the former develop to maturity.

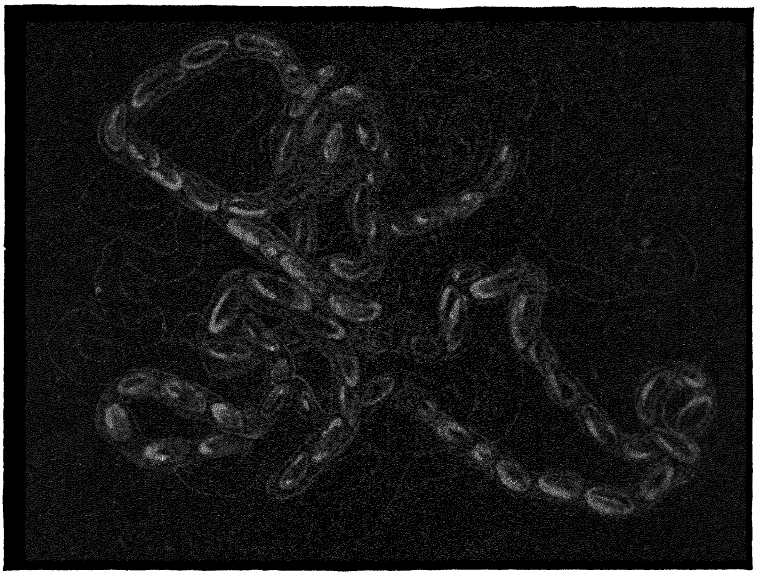

FIG. 168.—TWO POLYEMBRYONIC CHAINS EACH DERIVED FROM A SINGLE EGG OF *AGENIASPIS FUSCICOLLIS* AND CONTAINED IN THE SAME HOST.

One of the chains is viewed by reflected light and the other is represented in outline only. *After* Marchal, *Arch. Zool. Exp.*, 1904.

In the Proctotrypoidea polyembryony occurs in *Polygnotus* and *Platygaster*, whose hosts are Cecidomyidæ which are parasitized either as larvæ or eggs (Marchal, 1904; Leiby and Hill, 1923, 1924). *Platygaster hiemalis* which parasitizes the Hessian Fly is of special interest since some of its eggs develop into single embryos and others give rise to two embryos (Leiby and Hill). Apparently all the eggs develop in a similar manner up to the stage when four embryonic nuclei are present. If the egg is to form a single individual the embryonic area does not divide : where two embryos are formed separation of the blastomeres into two groups occurs. A trophamnion is formed in either event and it is clear that polyembryony has arisen from an already specialized method of monembryonic development.

In the Ichneumonoidea polyembryony is only known in two species of the Braconid *Macrocentrus* which parasitizes Lepidopterous larvæ. In *M. gifuensis* each egg produces up to eight or ten larvæ (Parker) while in *M. ancylivorus* only a single polyembryonically produced larva survives in a given host individual (Daniel). Among Vespoidea polyembryony occurs in the Dryniid wasp, *Aphelopus theliæ,* a parasite of Membracidæ (Kornhauser). The full details of the process have not been studied but a single egg is stated to produce about 50 embryos.

When a single parasite egg is laid in a given host the individuals of the polyembryonically produced offspring are either all females or all males, depending upon whether the original egg was fertilized or not. Often a progeny containing members of both sexes results and this fact is accounted for on the basis of more than one parasite egg having been laid in the host. Giard noted that nearly 3,000 individual *Litomastrix* may emerge from a single *Plusia* larva : both sexes were represented and it is certain that so large a progeny was not derived by the division of one egg.

Outside the parasitic Hymenoptera polyembryony has only been recorded in *Halictoxenos* (Strepsiptera). In their very brief preliminary account Noskiewicz and Poluszynski (*C.R. Soc. Biol. Paris,* 90, 1924, p. 896) state that the egg may divide into over 40 embryos.

Hermaphroditism.—Functional hermaphroditism is an extremely rare phenomenon in insects but is a regular feature in the Coccid *Icerya purchasi* (Hughes-Schrader, 1925, 1927). This species consists of true hermaphroditic individuals which correspond in general appearance and behaviour to the females of related species. They develop from fertilized eggs and are always diploid in chromosomal constitution. The hermaphroditic gonad is primarily an ovary and is formed by the fusion anteriorly of two originally separate organs. The outer cells of the gonad form the ovarioles, while those forming the central core of the organ become reduced to the haploid condition and form sperms. Fertilization of the eggs of the hermaphrodite by its own sperms gives rise to diploid embryos which develop into hermaphrodites. If the eggs remain unfertilized they develop pathenogenetically into haploid males. These males are only occasional and their copulation with hermaphroditic individuals is not necessary for reproduction.

Non-functional, accessory hermaphroditism is also very rare but is found in the stone-fly *Perla marginata.* Schœnemund (vide p. 264) has shown that all the males of this species possess a well-developed ovary connecting the anterior extremities of the testes. The eggs in this ovary show the male chromosomal number (22), and although they develop up to a late period they neither mature nor function (Junker, *Arch. f. Zellforsch.* 17, 1923).

As stated on p. 664, hermaphroditism in the fly *Termitoxenia* is not proven. Assmuth (1923) lays stress on there being no known males and on the fact that the vagina of the female bears an unpaired testis-like organ containing spermatozoa. Decisive evidence of spermatogenesis is, so far, wanting while the possibility that the organ in question is a spermatheca should not be overlooked.

Castration

Castration in the broad sense implies any process which interferes with or inhibits the production of ripe ova or spermatozoa in the gonads of an organism (vide Wheeler 1910: Salt, 1927).

Surgical Castration.—By this term is meant the sudden and complete extirpation of the gonads by artificial means. The experiment has been carried out by several observers and the insects successfully operated upon were lepidopterous larvæ in the 1st or later instars and crickets in the late nymphal period. The individuals on reaching the adult condition did not exhibit any deviations from the normal with regard to their instincts, and the development of their secondary sexual characters was in no way impaired by the absence of the gonads. In other cases, where the original operation was followed by the implantation of the gonads of the opposite sex, the secondary sexual characters of the original sex remained unaltered, even though they had not developed at the time of the operation.

The above experiments render it doubtful whether sex hormones occur in insects. The effects of parasitic castration (p. 541) suggest, however, that they may exist but that their origin is not in direct relation with the gonads (see Koller, *l.c.*, p. 139).

Physiological Castration.—Under this category are included certain forms of inhibition of the development of the gonads, leading to functional disability, brought about by an insufficient supply of nutriment. The best examples are met with among the social Hymenoptera where the majority of the female larvæ of a colony become workers and, owing to their inadequate nutrition, their ovaries remain in a very rudimentary state. This condition may be maintained throughout the adult life of the workers. If, on the other hand, the trophic status of the colony becomes highly favourable, or if the queen dies, one or more of the mature workers may functionally replace the latter, their ovaries undergoing active growth and producing fertile eggs owing, it is believed, to the influence of a special diet.

Parasitic Castration.—The influence of parasites in suppressing the reproductive function of their hosts was first adequately recognized by Giard. The hosts also undergo certain correlated structural changes and may assume characters of the opposite sex. The parasitization by *Stylops* of bees of the genus *Andrena* results in the female bees becoming sterile, and also involves the atrophy of the pollen-collecting apparatus, and the acquisition of the clypeal coloration of the male. In the males the changes that occur are less pronounced features. Modifications of the secondary sexual characters owing to the presence of strepsipterous parasites also occur in some wasps (*Odynerus*, *Chlorion* and *Sphex*). According to Salt (1927, 1931) these effects produce, or tend to produce, an actual interchange of those characters so that the parasitized individuals are to be regarded as intersexes. The Membracid *Thelia* when parasitized by a species of *Aphelopus* exhibits marked alterations (Kornhauser, 1919). The gonads in both sexes usually degenerate, and often disappear, while the genitalia suffer reduction. The males take on female characters as regards pigmentation and the shape and texture of the abdominal segments. Other examples of parasitic castration occur in species of *Typhlocyba* when infested by *Aphelopus* or by the Pipunculid fly *Chalarus*. Although the genitalia may become reduced as the result, there is no tendency of any parts to partake of characters belonging to the opposite sex. The parasitic nematode

Sphærularia has long been known to cause sterility in the hibernating queens of *Bombus*. Recently Goodey (1930) has described the life-cycle of the Nematode *Tylenchinema oscinellæ*, whose females enter the larvæ of the frit fly and reproduce in the imagines of that insect. The presence of these parasites inhibits growth of the gonads of the host and the sex cells fail to develop. No effects upon the secondary sexual characters of the host were, however, to be observed.

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Part II

DEVELOPMENT AND METAMORPHOSIS

Oviposition or egg-laying takes place among insects in diverse ways: the eggs are often protected in some manner or other, and are generally deposited in situations expressly adapted for the immediate needs of the subsequent offspring. In some cases the female simply drops the eggs at random while flying low, as happens for example in a few Lepidoptera whose larvæ feed on grasses or their roots. In very numerous instances they are laid singly, or in clusters, on the leaves of the future larval food-plants (Heteroptera, Lepidoptera, certain Coleoptera) : or they may be superficially inserted into plant tissues (Locustidæ, many Homoptera). When inserted more deeply excrescences (galls) of the plant may arise (Tenthredinidæ, Cynipidæ). In the Chrysopidæ they are laid at the apices of stiff pedicels made of a hardened secretion. In certain cases the eggs may be glued to some surface, in others they are laid beneath a web or a cottony covering. There are again insects which enclose their eggs either singly (Phasmidæ) or collectively (Mantidæ, Blattidæ) in a firm capsule or *ootheca*. Many aquatic species surround the eggs with a gelatinous secretion which swells in water forming a jelly-like spawn (Trichoptera, *Chironomus*). A considerable number of insects lay their eggs beneath the soil (Gryllidæ, many Coleoptera). Parasitic species oviposit on or within the bodies of the hosts which support their future offspring (Tachinidæ, parasitic Hymenoptera) : when the host is a vertebrate, the eggs are often fastened to the hair or feathers (Anoplura, Œstridæ).

Embryonic development may take place entirely after oviposition, or partly while the eggs are still within the parental body, or the whole phase may be passed within the latter (in viviparous species). Almost every transition between these conditions may be found, notably among the higher Diptera. The duration of the egg state (after oviposition) is very variable. In some of the Sarcophaginæ it is only momentary, the larva emerging immediately : in *Musca domestica* it lasts about 8–12 hours, according to temperature. At the other extreme are certain Lepidoptera which pass about nine months in the egg, and among the Phasmidæ this stage may last nearly two years.

In discussing the development of insects the subject falls naturally into two divisions : (*a*) embryology and (*b*) post-embryonic development.

EMBRYOLOGY

IN the eggs of most insects there is a distinction between the anterior and posterior poles which bears a definite relation to the position of the future embryo. The eggs are located in the ovarioles in such a position that the cephalic pole of each is directed towards the head of the parent: also, the dorsal and ventral aspects of the egg correspond with those of the parent and of the future embryo (Hallez, 1886). This relationship becomes less evident in the more spherical eggs but there is every reason to believe that it holds good.

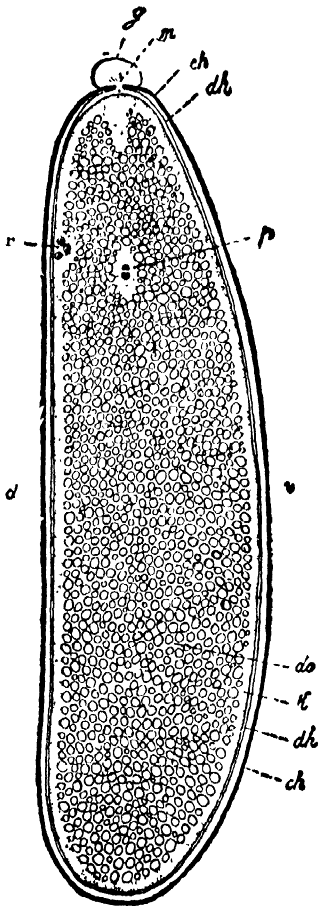

FIG. 169.—LONGITUDINAL SECTION OF THE EGG OF *MUSCA* IN STAGE OF FERTILIZATION.

ch, chorion; *d*, dorsal, *v*, ventral side; *dh*, vitelline membrane; *do*, yolk; *g*, gelatinous cap over micropyle (*m*); *k*, periplasm; *p*, male and female pronuclei; *r*, polar bodies. *From* Korscheldt and Heider after Henking and Blochmann.

The contents of the egg are made up of two portions, namely, protoplasm, and deutoplasm or yolk. The protoplasm forms a reticulum which pervades the substance of the egg and also forms a bounding layer, or *periplasm*, which lies just beneath the vitelline membrane, and completely surrounds the egg (Fig. 169). The *deutoplasm* is contained within the meshes of the protoplasm and consists of vitelline spheres and generally globules of fat: small refringent vitelline bodies are present within the vitelline spheres. In addition to these constituents many eggs contain minute greenish bodies known as Blochmann's corpuscles, which are independent organisms capable of cultivation in artificial media.

In the unfertilized egg the germinal vesicle, or nucleus, is situated in the central part of the yolk, enclosed in an island of protoplasm. During the maturation process the germinal vesicle migrates towards the periphery of the egg where it undergoes division and the polar bodies are formed (Fig. 169). After fertilization the zygote nucleus passes inwards and there commences to divide into daughter nuclei.

Cleavage and Blastoderm Formation.—The products of the division of the zygote nucleus are the cleavage nuclei, each of which becomes enveloped by a stellate mass of protoplasm. When a considerable number of cleavage cells have been formed, the majority migrate to the periphery of the egg, where they become merged with the periplasm (Fig. 170). In this manner they form a continuous cellular layer or *blastoderm* surrounding the yolk (Fig. 171). At a slightly later stage the blastoderm consists of a layer of columnar cells (*ventral plate*) on the ventral side of the egg and a flattened epithelial stratum over the remainder (Fig. 172).

Those of the cleavage cells which remain in the yolk form the *primary yolk cells*, which become augmented by *secondary yolk cells* derived by the immigration of cells from the blastoderm. In some cases it appears that the yolk cells are only derived from the latter source. Among several orders of insects, notably Orthoptera, Lepidoptera and Coleoptera the yolk undergoes secondary cleavage, becoming thereby divided into polyhedral masses each of which contains one or

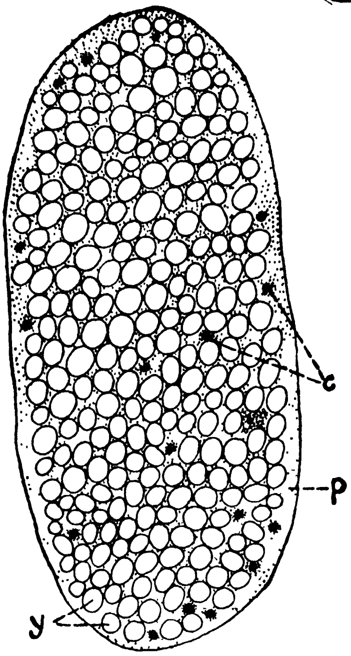

FIG. 170.—LONGITUDINAL SECTION OF THE EGG OF *CLYTRA LÆVIUSCULA*, 24 HOURS OLD.

The cleavage cells (*c*) are seen migrating towards the periphery of the egg. *p*, periplasm; *y*, yolk spheres. *After* Lecaillon.

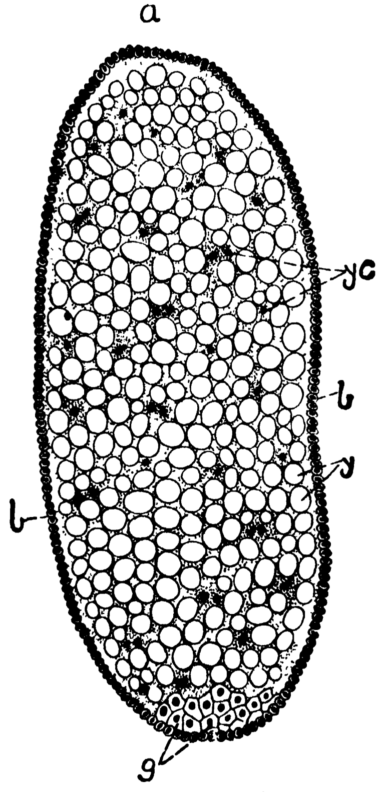

FIG. 171.—MEDIAN LONGITUDINAL SECTION OF THE EGG OF *CLYTRA LÆVIUSCULA* AT THE TIME OF COMPLETION OF SEGMENTATION.

a, anterior pole; *b*, blastoderm; *g*, genital cells; *y*, yolk spheres; *yc*, yolk cells. *After* Lecaillon.

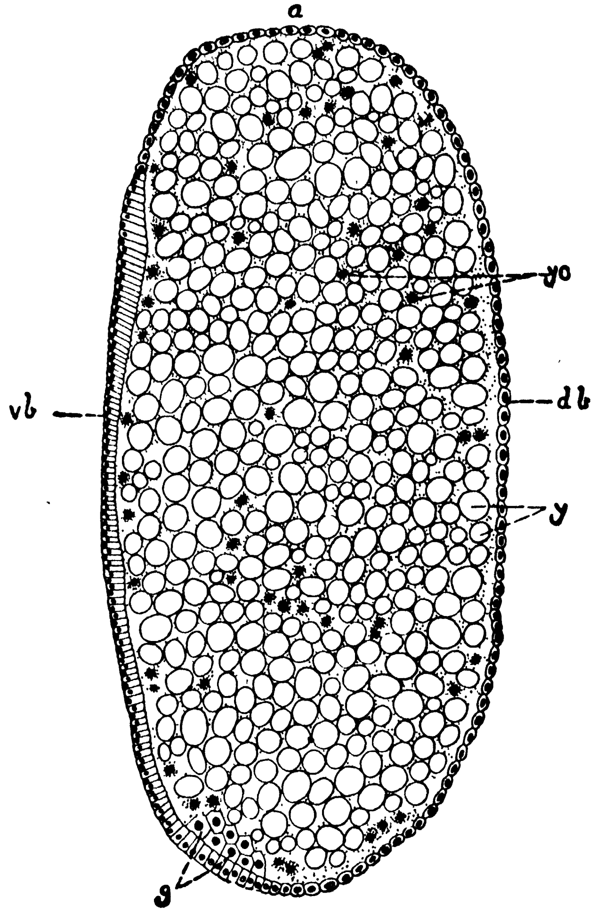

FIG. 172.—MEDIAN LONGITUDINAL SECTION OF THE EGG OF *CLYTRA LÆVIUSCULA* AT THE TIME OF DIFFERENTIATION OF THE ECTODERM.

db, dorsal blastoderm; *vb* ventral blastoderm. Other lettering as in Fig. 159. *After* Lecaillon.

more yolk nuclei (Fig. 176). The function of the yolk cells is to liquefy the yolk and bring about its assimilation.

In a few insects the cleavage is total rather than peripheral as described above. This feature is exhibited among Collembola (e.g. *Anurida*) and certain of the endoparasitic Hymenoptera. In the former example the cleavage is slightly unequal and subsequently becomes peripheral: this condition is probably ancestral to the usual type found among insects. Among the parasitic Hymenoptera the cleavage is total and complete which has probably been secondarily acquired in relation to the almost entire absence of yolk.

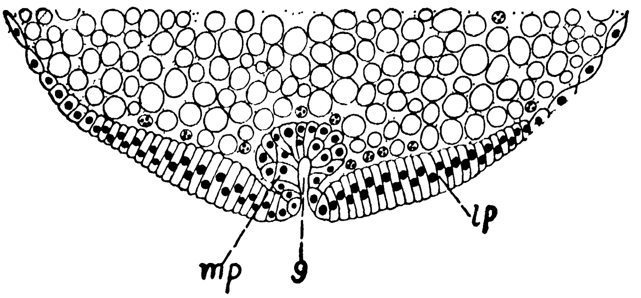

Fig. 173.—Transverse Section of the Germ-Band of *Clytra læviuscula* at the time of Formation of the Gastral Groove (*g*).

lp, lateral plate; *mp*, median plate. *After* Lecaillon.

Formation of the Germ Band.— The *germ band* makes its first appearance as the ventral plate already alluded to. The extent of the germ band depends upon the amount of yolk present. When very abundant the germ band occupies a relatively small area: with eggs poor in yolk, as in Diptera the germ band extends along the whole ventral surface, and its two extremities nearly meet on the dorsal aspect of the egg.

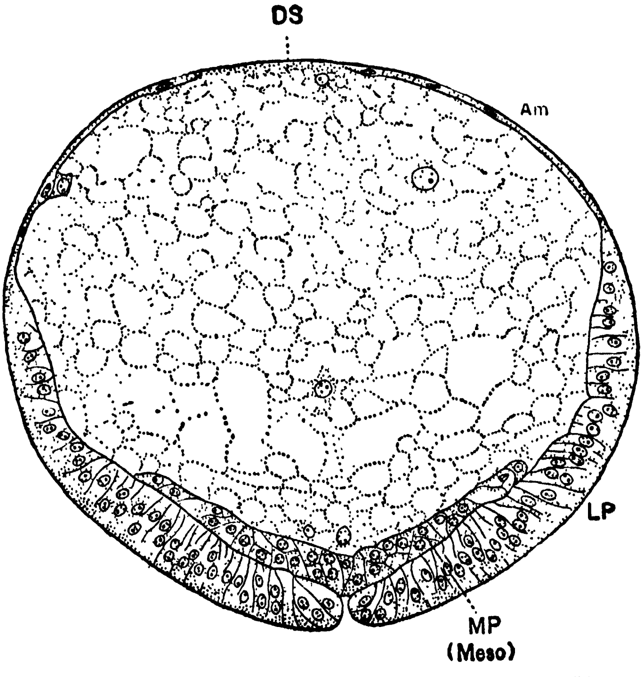

Fig. 174.—Transverse Section of Egg of the Honey Bee.

MP, middle plate; *LP*, lateral plate; *Am*, amnion; *DS*, dorsal strip of blastoderm. *After* Nelson, 1915.

A pair of longitudinal folds appears on either side of the median line of the ventral plate which thus cut off a *middle plate* and two *lateral plates* (Fig. 173). In most insects (e.g. *Hydrophilus, Musca, Donacia,* etc.) a groove-like invagination (*gastral groove*) extends the whole length of the middle plate, representing a modified process of gastrulation, while the actual mouth of the groove is the homologue of an elongate blastopore. The lateral folds grow over the middle plate and the groove becomes converted into a tube: or, the overgrowth may take place in such a way that the cavity of the groove is wholly, or partially, obliterated. The tubular cavity, when present (as in *Hydrophilus*), is evanescent and is the counterpart of the archenteron of other animals. In some insects (e.g. *Apis, Pieris, Gastroidea,* etc.) the middle plate remains flat, and is overgrown by the lateral folds, without any invagination being formed (Fig. 174). In either event, the meeting of the lateral folds results in the production of a two-layered germ band. The lateral plates give rise to the ectoderm, and the *inner layer* (formed from the middle plate) is the rudiment of the future mesoderm. In a third type the inner layer results from a simple proliferation of the ectoderm along the median line of the ventral plate (Apterygota and Orthoptera) and may, or may not, be accompanied by the formation of a gastral groove.

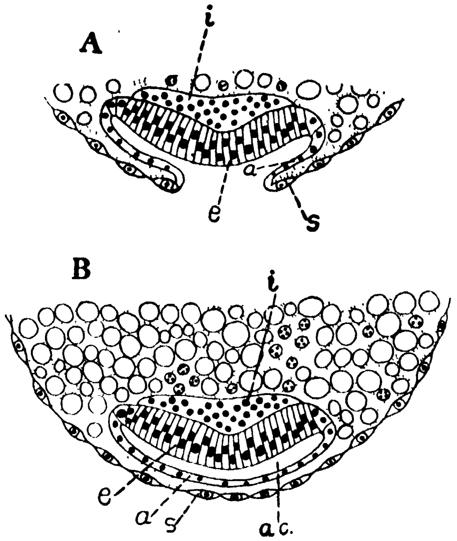

FIG. 175.—A, TRANSVERSE SECTION OF THE GERM-BAND OF *CLYTRA* AT THE TIME OF FORMATION OF THE AMNIOTIC FOLDS. B, AT THE TIME OF FUSION OF THE AMNIOTIC FOLDS.

a, amnion ; *ac*, amniotic cavity ; *e*, ectoderm ; *i*, inner layer (mesoderm) ; *s*, serosa. Based on Lecaillon.

The Embryonic Envelopes and Blastokinesis.—It is characteristic of insects that the germ band does not remain freely exposed on the surface of the yolk but becomes covered by *amniotic folds* arising from its edges. These folds grow towards one another, usually meeting and fusing, with the result that they enclose a space or amniotic cavity containing the germ-band (Fig. 175). It will be observed from reference to Fig. 175 that the germ-band becomes covered by a double cellular envelope composed of the *amnion* and *serosa*. The *amnion* or inner envelope is continuous with the margins of the germ-band, while the *serosa* is an extension of the undifferentiated blastoderm covering the surface of the yolk, and forms the outer envelope to protect the developing embryo.

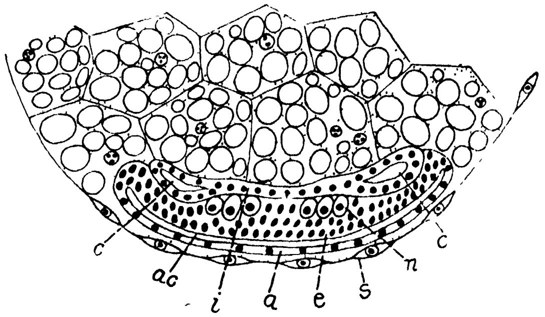

FIG. 176.—TRANSVERSE SECTION OF THE GERM-BAND OF *CLYTRA* AT THE TIME OF APPEARANCE OF THE NEUROBLASTS (*n*) AND CŒLOMIC CAVITIES (*c*).

Other lettering as in Fig. 175. *After* Lecaillon.

The formation of the embryonic envelopes presents many variations which are dependent upon whether the germ-band is invaginated into the yolk, simply immersed in the latter, or lies wholly superficially to the yolk.

Insects with an invaginated germ-band are exemplified by certain of the Thysanura, the Odonata and many Hemiptera and Orthoptera. In *Lepisma* the germ-band becomes segmented at the same time as it is being bodily sunk into the yolk, and the invagination, or amniotic cavity, remains permanently open by means of the amniotic pore (Fig. 177). The yolk is almost entirely covered by the serosa which is characterized by its large and widely spaced-apart nuclei. The inner walls of the cavity consist of ordinary flattened cells with normal nuclei and constitute the amnion.

At a later stage the embryo becomes completely everted and superficial in position. In *Machilis* the embryo is very similarly invaginated, but the front half of the egg exhibits the characteristic serosa cells, while the hinder half remains covered by cells with ordinary nuclei which represent the amnion. In the dragonfly *Calopteryx* the germ-band gradually sinks, at its hinder extremity, into the yolk and the space thus formed is the amniotic cavity (Fig. 178). As the germ-band sinks deeper, a portion of the undifferentiated blastoderm is drawn in with it, and forms the amnion. The part of the blastoderm not drawn into the cavity, but remaining around the yolk, constitutes the serosa. The invagination of the germ-band, or embryo as it now may be termed, proceeds in such a manner that its ventral surface comes to lie towards the dorsal aspect of the egg, and its posterior extremity is directed towards the anterior pole. The cephalic portion of the embryo remains in its superficial position for a while, but it subsequently becomes enveloped by ventral folds of the amnion. The latter meet, completely enclosing the embryo, and at their point of union the amnion fuses with the serosa. Except just at the latter position, the two embryonic envelopes are separated by yolk. When the process is complete the original position of the whole embryo is reversed, and it will be observed that the dorsal and side walls of the amniotic cavity are formed by the amnion while the ventral wall is formed by the embryo itself. At a later stage the embryo undergoes further changes in position during which great alterations take place in the amnion and serosa. The latter contracts and thickens, drawing all the yolk towards the anterior pole. The increase of pressure that is consequent, together with the growth of the embryo, causes the amnion to rupture at the point of its fusion with the serosa. As the latter goes on contracting, the head of the embryo protrudes through the split and, turning round, becomes directed towards the anterior pole of the egg. The rest of the embryo follows in due course, and it eventually comes to lie in its original ventral position. These movements of the embryo are termed *blastokinesis*. To recapitulate, the germ-band always arises on the ventral surface of the yolk, and it moves through an arc until its position is completely reversed on the dorsal surface. Here it rests for a while, and again passes through the same arc to its original ventral position. Blastokinesis is characteristic of the Exopterygota whose eggs are rich in yolk, and the germ-band is invaginated therein: in eggs poorer in yolk the process is usually less marked or wanting (vide Wheeler, 1893: Henneguy: Heymons, 1895).

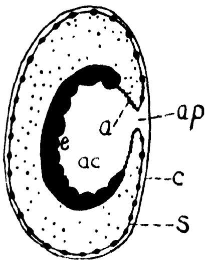

FIG. 177.—DIAGRAM OF THE EMBRYO AND EMBRYONIC MEMBRANES IN *LEPISMA* ACCORDING TO HEYMONS.

a, amnion; *ac*, amniotic cavity; *ap*, amniotic pore; *c*, chorion; *e*, embryo, *s*, serosa.

In the superficial type of germ-band the embryo retains its ventral position and blastokinesis is usually wanting. The embryonic envelopes are formed as overfolds of the germ-band arising from the edges of the latter at its anterior and posterior extremities: the cephalic and caudal folds are generally connected later by side folds. When the folds come into apposition their intervening walls fuse, and two continuous embryonic membranes are formed which enclose an amniotic cavity on the ventral aspect of the embryo. This type of germ-band is well exhibited, for example, in Diptera Orthorrhapha and among Hymenoptera.

In Lepidoptera and the Tenthredinidæ the envelopes develop in a similar nanner, but the germ band subsequently sinks bodily into the yolk and he latter enters between the amnion and serosa. In this manner the mmersed type of germ band is produced.

Among Coleoptera (*Hydrophilus*, *Gastroidea*, *Melasoma*) the development s intermediate between that of *Calopteryx*, with a completely invaginated erm-band, and the wholly superficial type. The posterior extremity of he germ-band becomes invaginated after the manner already described

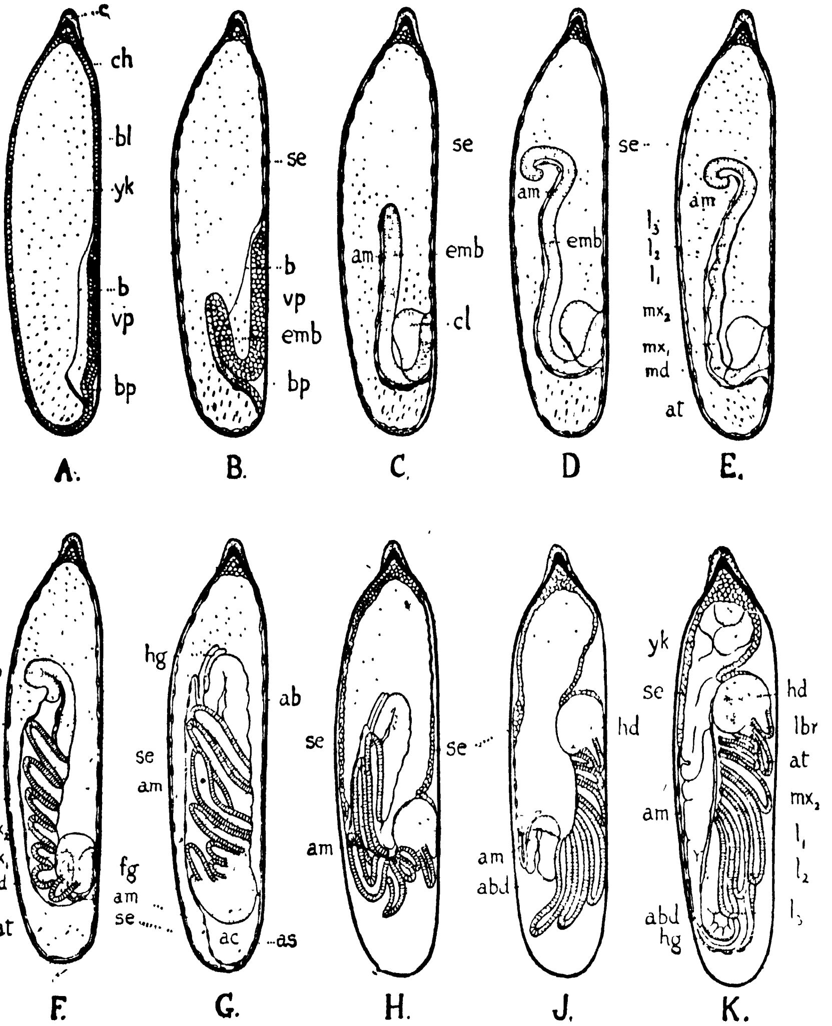

FIG. 178.—STAGES IN THE EMBRYONIC DEVELOPMENT OF *CALOPTERYX*.

Lateral view, ventral surface to the right. A, Formation of ventral plate. B—D, Invagination of embryo in yolk. —G, Formation of appendages. H—K, Rupture of amnion and reversion of embryo. *ab*, abdomen; *ac*, amniotic avity; *am*, amnion; *as*, union of amnion and serosa; *at*, antenna; *b*, lateral border of ventral plate; *bl*, blastoderm; *b*, blastopore; *c*, cap or pedicel; *ch*, chorion; *cl*, cephalic lobe; *emb*, embryo; *fg*, stomodæum; *hd*, head; *hg*, procto-æum; *l₁–l₃*, legs; *lbr*, labrum; *md*, mandible; *mx*, first maxilla; *mx₂*, labium; *se*, serosa; *vp*, ventral plate; *yk*, olk. From Tillyard, *Biology of Dragonflies*, *after* Brandt.

or *Calopteryx*, bending round dorsally and becoming immersed in the olk. Both anterior and posterior amniotic folds develop and fuse in the sual manner, thus enclosing the embryonic area. Finally the posterior xtremity becomes drawn out of the yolk and regains its superficial position. his migration of the germ-band is to be regarded as a vestige of the process f blastokinesis, and the type of development is probably derived from ncestors in which the whole germ-band was invaginated. As Korschelt nd Heider suggest, it is likely that the invaginated germ-band is the primitive one, while the superficial type, which is wholly overgrown by amniotic folds, is a secondary condition. With the acquisition of the latter blastokinesis becomes no longer evident.

In the Locustidæ a third envelope or *indusium* appears as a disc-like thickening of the blastoderm, just in front of the future head (Fig. 179). It develops into a membrane which pushes its way between the serosa and the yolk, finally becoming an inner envelope next the yolk and only separated from the embryo by the amnion. This structure itself forms a second membrane or outer indusium and the two membranes cover the whole surface of the egg except at the poles: they subsequently shrink and disappear with the growth of the embryo. The precephalic organ of Collembola, which has a similar mode of initial development, has been homologized with a degenerate indusium (vide Wheeler, 1893).

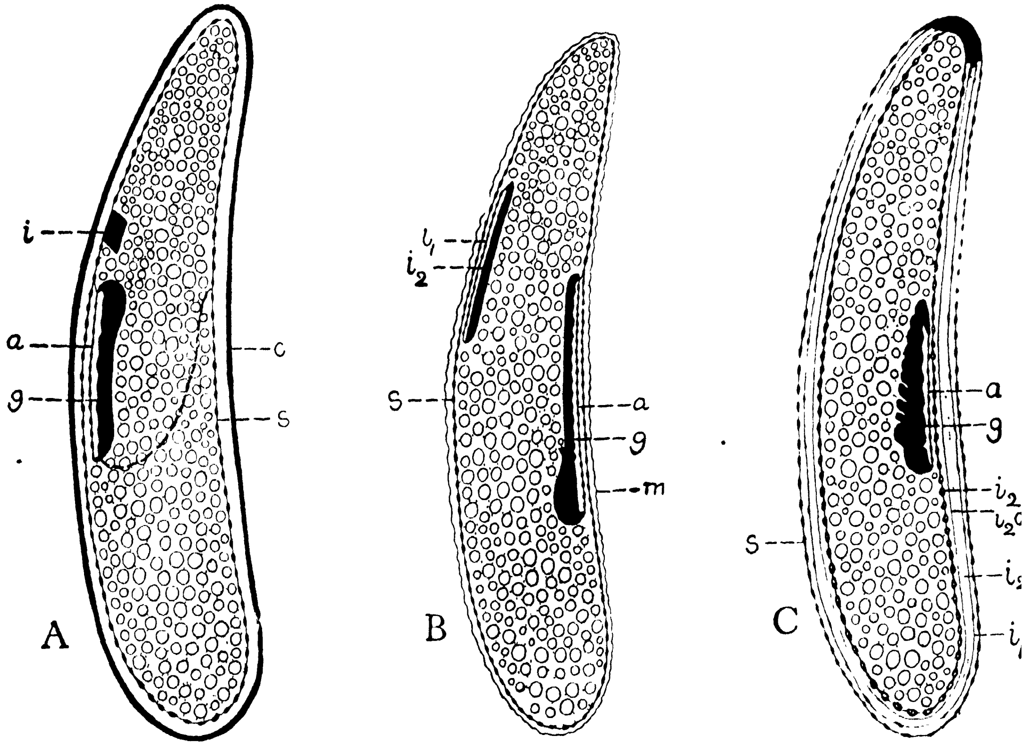

FIG. 179.—FIGURES ILLUSTRATING THE MOVEMENTS AND ENVELOPES OF THE EMBRYO OF *XIPHIDIUM*

A, after closure of amnioscrosal folds; the broken line shows the path of migration of the embryo.
B, embryo on dorsal surface.
C, shortening of embryo.
a, amnion; *c*, chorion; *g*, germ band; *i*, indusium; i_1, outer indusium; i_2, inner indusium; i_2c, cuticle and i_2s, granular secretion of inner indusium. *After* Wheeler, *Journ. Morph.*, 3.

In addition to the foregoing there are certain anomalous types. An amnion and serosa are totally wanting in *Anurida* and other Collembola, and are vestigial in the higher Diptera. In *Apis* there is a single envelope homologous with a serosa (Nelson). In many parasitic Hymenoptera the egg is surrounded by a single envelope known as the trophamnion. It is composed of a small number of large cells with prominent nuclei and may persist up to the time of the eclosion of the larva. In any event it breaks down and, in some cases, its cells afterwards occur free in the blood of the host. Its method of development differs in various species: in *Litomastix* and the Platygasteridæ it is formed from the polar bodies (Silvestri, 1906, 1921) or at the commencement of cleavage (Marchal, 1906). In *Litomastix* a second membrane, formed by delamination of the blastoderm, is present (Silvestri).

Formation of the Embryo.—At an early stage in development the germ-band becomes divided by means of transverse furrows into a series of segments and, in this condition, it may be referred to as the embryo (Figs. 180–182). The segmentation may even occur contemporaneously with the formation of the gastral groove, as in *Hydrophilus* and *Chalicodoma*, but as a rule it does not become apparent until after the separation of the inner germ layer. The embryo is at first divisible into a *protocephalic* or *primary head region*, and a *protocormic* or *primary trunk region.* The protocephalic region is conspicuous on account of its large lateral lobes, which give rise to the *protocerebral* or *ocular segment*. The latter bears evanescent *pre-antennal appendages* in *Carausius* (Wiesmann, 1926), but such organs have not so far been detected in any other insect. Immediately in front of the ocular segment is a median and often bilobed swelling which is the future *labrum*. It is not regarded as a true segment but rather as a pre-oral outgrowth—the acron of Heymons. The second primary head segment is the *deutocerebral* or *antennary segment* which bears a pair of outgrowths representing the future antennæ. The third segment is the *tritocerebral* or *intercalary segment*: in some cases it bears a pair of evanescent rudimentary appendages (Fig. 183, A) homologous with the Crustacean 2nd antennæ and in *Campodea* vestiges of them are retained in the adult (Uzel). Immediately behind the labrum is a pit-like invagination of the ectoderm which is the beginning of the future stomodæum. The first three of the primary trunk segments subsequently combine with the protocephalic region to form the future head. These segments are those which bear the developing rudiments of the mandibles and 1st and 2nd maxillæ. The *maxillary segment* also bears a median protuberance which gives rise to the hypopharynx and, in *Anurida* and *Campodea*, a pair of small protuberances situated near the median line are the rudiments of the future *superlinguæ* (Fig. 183, B). The appendages of the *2nd maxillæ* ultimately fuse to form the *labium.* The next three protocormic segments bear the rudiments

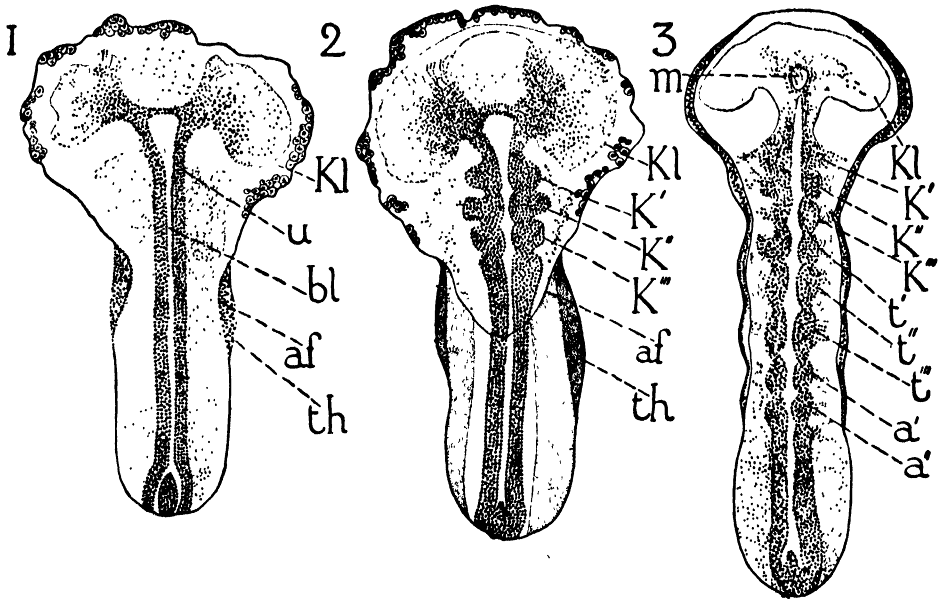

FIG. 180.—THREE STAGES IN THE SEGMENTATION OF THE GERM-BAND OF A LEAF-BEETLE (*MELASOMA*).

a'a'', abdominal segments; *af*, amniotic fold; *bl*, blastopore; *k'–k'''*, gnathal segments; *kl*, head-lobe; *t'–t'''*, thoracic; segments. *After* Graber.

of the future three pairs of *thoracic legs* and eventually form the thorax, while the remaining segments constitute the abdomen. In most insect embryos the latter region consists of ten segments, together with a terminal region or *telson*. The telson bears a median invagination which is the beginning of the proctodæum. There is good reason to believe, however, that the primitive number of abdominal segments was 12; this number having been recognized by Heymons in the embryos of Dermaptera, Orthoptera and Odonata, and by Nelson in that of the hive bee. All the abdominal segments, excepting the telson, may carry a pair of embryonic appendages and, in some orders, the first pair is frequently much more pronounced than those on the remaining segments and later may take on a peculiar structure. According to Wheeler (1889A) this pair of appendages was possibly glandular in function and formerly had an important significance. In the Apterygota one or more pairs of the abdominal appendages persist throughout adult life: among other insects they remain as the abdominal feet of larval Tenthredinidæ and Lepidoptera, and as gills in the larvæ and nymphs of certain aquatic groups. As a rule, however, all traces of abdominal appendages disappear on hatching, with the exception of the last pair which is retained in many orders as the *cerci*. It is still a disputed point as to whether the gonapophyses are to be regarded as true appendages or not. As pointed out on p. 48, the outer pair on the 9th abdominal segment is to be regarded as derived from abdominal limbs, while the remaining gonapophyses are most probably secondary developments.

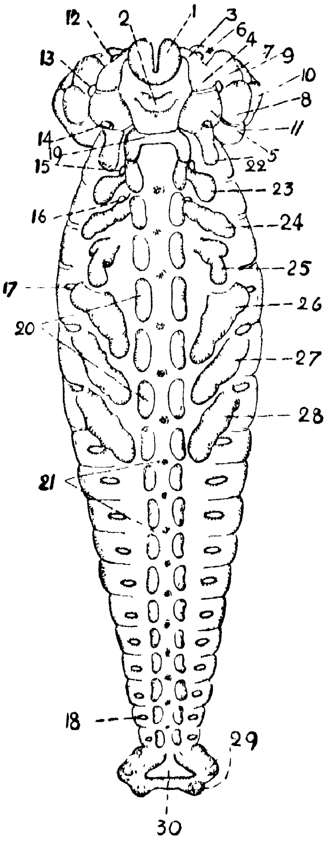

FIG. 181.—EMBRYO OF *LEPTINOTARSA*.

1, labrum; 2, stomodæum; 3–5, brain segments; 6–8, segments of optic ganglion; 9–11, segments of optic plate, 12–16, tentorial invaginations, etc; 17, 18, first and last spiracles; 19, tritocerebral commissure; 20, neuromeres; 21, middle-cord thickenings; 22, antenna; 23, mandible; 24, maxilla; 25, labium; 26–28, legs; 29, rudiments of Malpighian tubes, 30, proctodæum *After* Wheeler, *Journ. Morph* 3.

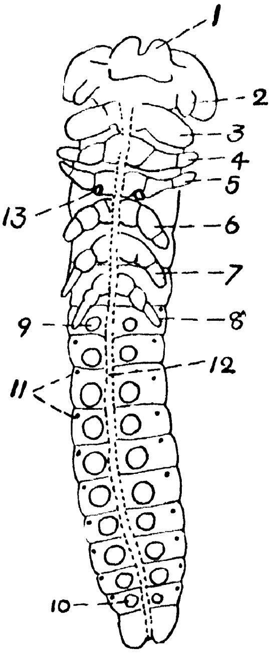

FIG. 182.—EMBRYO OF SILK WORM.

1, labrum; 2–5, head-appendages; 6–8, legs; 9, 10, first and last abdominal appendages; 11, spiracles; 12, neural furrow; 13, opening of silk gland on labium. *After* Toyama, *Bull. Agric. Coll. Tokyo*, 5.

Dorsal Closure of the Embryo and Degeneration of the Embryonic Envelopes.—As the embryo develops it grows round the yolk and the dorsal or non-embryonic portion of the blastoderm becomes more and more restricted. The final closure and the fate of the embryonic membranes exhibit important differences among various insects which are classified by Korschelt ~~and~~ Heider into four main types.

1. INVOLUTION THROUGH THE FORMATION OF A DORSAL AMNIOSEROSAL SAC.—This process occurs in the more generalized orders of Pterygota but exhibits various modifications. The two envelopes rupture and, with the upward growth of the embryo, their contracted remains become carried on to the dorsal side of the yolk. Here they sink into the latter, forming a tubular sac known as the *dorsal organ*. Ultimately the dorsal organ undergoes dissolution and the embryonic ectoderm completes the dorsal closure. In *Hydrophilus* the two flaps formed by the rupture of the amnion and serosa become carried to the upper side of the yolk, with a small contracted area of the original dorsal serosa between them. The flaps then overgrow the latter until their edges unite. By this means a tubular dorsal organ is formed, which sinks into the yolk and becomes enclosed by the developing mesenteron, while the embryonic ectoderm completes the dorsal closure (Fig. 184, A–E). In *Œcanthus* the contracted serosa alone forms the dorsal organ, the amnion persisting, for a while, as a covering of the yolk (Fig. 184, A, B, F–H).

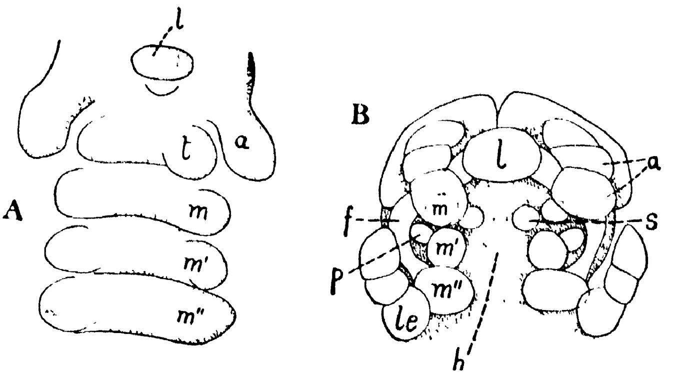

FIG. 183.—CEPHALIC REGION OF EMBRYO OF *ANURIDA* SHOWING DEVELOPING APPENDAGES.

A, at an early stage; B, later; *a*, antenna; *f*, oral fold; *h*, hypopharynx; *l*, labrum; *le*, leg; *m*, mandible; *m′*, maxilla; *m″*, labium; *p*, maxillary palp; *s*, superlingua; *t*, trito-cerebral appendage. *After* Folsom, *Bull. Mus. Zool. Harvard*, 30 (redrawn).

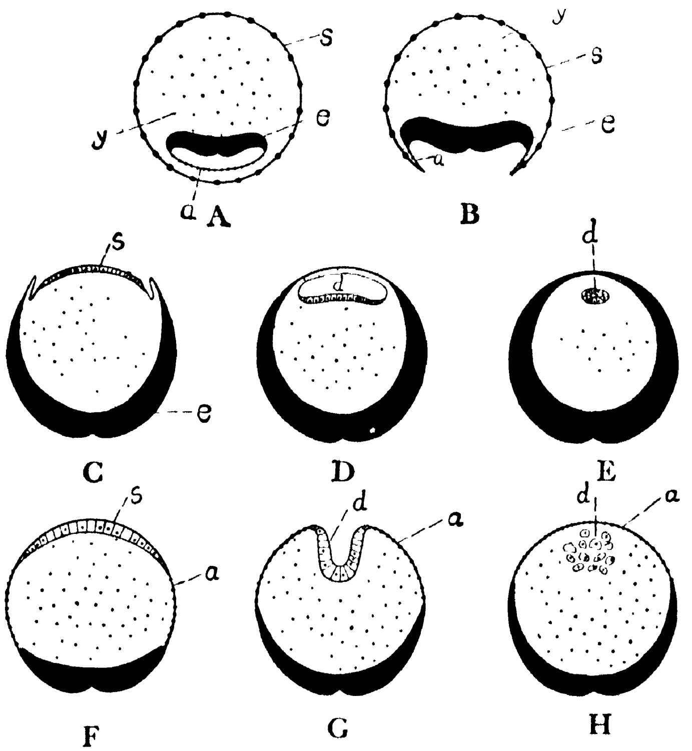

FIG. 184.—DIAGRAMS ILLUSTRATING THE DORSAL CLOSURE OF THE EMBRYO AND THE FATE OF THE EMBRYONIC MEMBRANES. A, B, GENERAL. C—E, *HYDROPHILUS*. F—H, *ŒCANTHUS*.

a, amnion; *d*, dorsal organ; *e*, embryo; *s*, serosa; *y*, yolk. Based on Ayers, Graber and Kowalevsky.

2. INVOLUTION OF THE AMNION WITH THE RETENTION OF THE SEROSA.—In *Leptinotarsa* and other of the Chrysomelidæ, the amnion ruptures ventrally and grows round the yolk so as to enclose it dorsally, becoming at the same time

separated from the serosa. With the upward growth of the embryo the amnion becomes compressed into a small dorsal tract—the *dorsal organ.* The latter disintegrates in the yolk with the dorsal closure of the embryo. The serosa persists, until a late stage, as a complete membrane applied to the inner aspect of the chorion (Fig. 185, A–C).

3. INVOLUTION OF THE SEROSA WITH RETENTION OF THE AMNION.—In *Chironomus* the serosa alone ruptures and contracts to form the dorsal organ, which becomes absorbed into the yolk. The amnion afterwards grows over this area, so as to entirely enclose the egg, and persists until the time of hatching (Fig. 185, D–F).

4. RETENTION OF BOTH THE AMNION AND SEROSA.—In Lepidoptera and Tenthredinidæ the amnion ultimately grows entirely round the yolk and becomes separated from the serosa. The egg is now enclosed by two complete envelopes up to the time of hatching, when they are ruptured. In Lepidoptera a quantity of yolk is retained between these two envelopes, which serves as the first food of the young larva (Fig. 185, G, H).

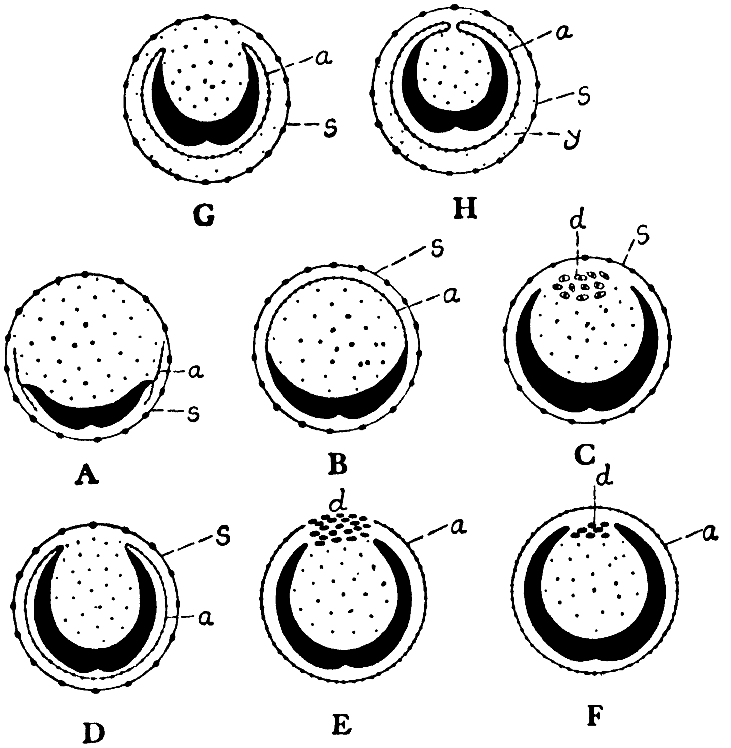

FIG. 185.—DIAGRAMS ILLUSTRATING THE DORSAL CLOSURE OF THE EMBRYO AND THE FATE OF THE EMBRYONIC MEMBRANES IN A—C, *LEPTINOTARSA*: D—F, *CHIRONOMUS*: G, H, LEPIDOPTERA.

Based on Wheeler, Graber and Tichomiroff.

The Mesoderm. — The whole of the inner layer, or that part of it which does not participate in endoderm formation, gives rise to the mesoderm. The latter becomes arranged into two longitudinal bands, connected across the median line by a single layer of cells. These bands come to be constricted transversely, and consequently the mesoderm is divided into segments which correspond with those of the ectoderm previously alluded to (p. 177). These divisions are the *mesoblastic somites* and, sooner or later, a pair of cavities or *cœlom sacs* appears in each (Figs. 176, 186). In their completely developed condition, as seen in *Carausius,* paired cœlom sacs are present in relation with the labrum and in each head segment and in every trunk segment up to, and including, the 10th abdominal segment—there are also vestiges in the 11th abdominal segment. In other generalized insects cœlom sacs are undeveloped in the labral and protocerebral segments, and it is apparent that an unusually primitive phase is displayed in the development of *Carausius.* In the higher insects the mesoblastic somites show secondary modifications: thus, in the Muscidæ they remain solid throughout, while in the hive bee Nelson finds that the cœlom sacs on either side of the body are confluent, thus forming a pair of longitudinal tubes. The outer or somatic layer of the mesoblastic somites gives rise to the body muscles, dorsal diaphragm, and pericardial cells: from the inner or splanchnic layer the visceral muscles, genital ridges, and the greater part of the fat-body are produced. At the upper angles, where the somatic and splanchnic layers meet, are peculiar cells termed *cardioblasts* (Fig. 188) which take part in the formation of the heart. The middle layer of mesoderm, which unites the somites of the two sides of the body, appears in some insects to dissociate and form blood cells. The mesoderm of the protocerebral segment produces the musculature of the stomodæum, and a similar mass at the posterior end of the embryo provides the proctodæal musculature.

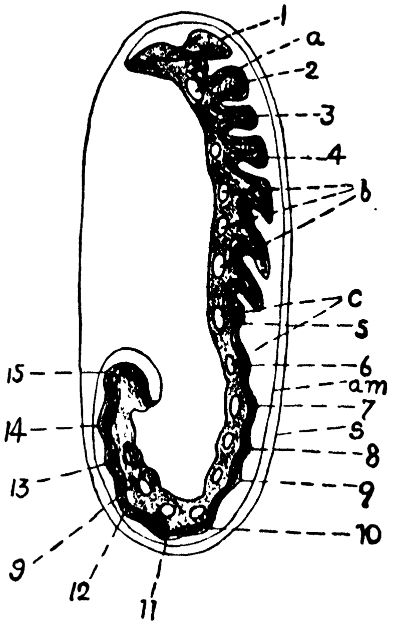

Fig. 186.—Diagrammatic Sagittal Section (a little to one side of the Median Line) of the Embryo of *Donacia crassipes* showing Cœlom Sacs.

1–4, cephalic appendages; 5–15, abdominal segments; *a*, cœlomic sac of intercalary segment; *b*, cœlom sacs of thoracic segments; *c*, cœlom sacs of abdomen; *am*, amnion; *s*, serosa; *g*, genital cells. Adapted from Hirschler, *Zeits. wiss. Zool.* 1909.

The Endoderm.—The origin of the endoderm is a much disputed problem of insect embryology and its method of development is, furthermore, subject to modification in different insects (vide Eastham, 1930A). In most cases it appears as two widely separated masses of cells which are applied to the blind ends of the stomodæum and proctodæum respectively (Fig. 187). These masses become U-shaped, and the arms of each U elongate and grow so that the two masses are joined by a pair of cell-strands. These latter grow together in the median line, and also extend laterally, so as to eventually extend round the yolk and form a complete tube which constitutes the *mesenteron*, or primitive mid-intestine. Some observers, including Hirschler, maintain that a middle section of endoderm is also formed between the two original masses.

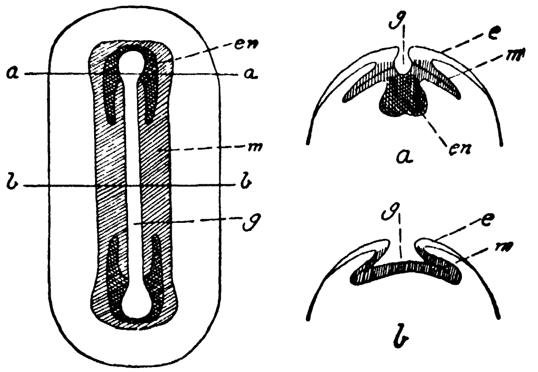

Fig. 187.—Diagram showing Endoderm Formation in *Leptinotarsa* according to Wheeler.

The sections on the right are taken across the germ-band where the lines bear similar lettering. *e*, ectoderm; *en*, endoderm; *g*, gastral groove; *m*, mesoderm.

A large number of competent embryologists state that the endoderm is derived from the inner layer. This view is held for example by Kowalevsky and Escherich for *Calliphora*, by Wheeler for *Phyllodromia* and *Leptinotarsa*, by Heider for *Hydrophilus*, by Grassi, Petrunkewitsch, and

Nelson for *Apis* and by Hirschler for *Donacia*. Another group of embryologists hold that the two masses of cells are derived by cell-proliferation taking place at the blind ends of the stomodæum and proctodæum. Its natural consequence is that the mesenteron is of ectodermal origin. This view was upheld by Ganin, Witlaczil and Voeltzkow, but its chief modern supporters are Lecaillon (for Coleoptera) and Heymons (for Orthoptera and Dermaptera). According to Heymons the functional mesenteron of the Pterygota is of recent origin, and the original endoderm is now represented by yolk cells which are to be regarded as representing a vestigial mesenteron. This view has received support from Heymons' discovery of the formation of the mesenteron from yolk cells in *Lepisma* and *Campodea*, and from Claypole's discovery of the same method of formation in *Anurida*. Tschuproff also states that in Odonata it is formed partly from the ectodermal invaginations, and partly from the yolk cells—the latter building up the middle section only. The view that the ectoderm produces the mesenteron in insects is completely at variance with what is known from a study of other classes of the animal kingdom. Definite proof is still needed to demonstrate that the cells around the blind ends of the stomodæum and proctodæum are actually derived from those invaginations, and not from cells of the inner layer which have become intimately associated with them at a very early stage. (It is also noteworthy that Nusbaum and Fulinski reinvestigated endoderm formation in *Phyllodromia* and *Gryllotalpa*, which were studied by Heymons, and came to the conclusion that it is derived from the inner layer.)

The Alimentary Canal.—The alimentary canal is formed in three sections. The anterior section or *stomodæum* is constituted by an ectodermal invagination at the anterior extremity of the germ band, while the posterior section or *proctodæum* is formed somewhat later by a similar invagination of the telson (Fig. 181). The middle section or mesenteron develops as a sac (previously described) which is situated between the blind extremities of these two ingrowths. The establishment of a through passage, from the mouth to the anus, is brought about by the absorption of the intervening walls where they are apposed to one another. The Malpighian tubes develop as paired outgrowths of the proctodæum, at a stage when the latter is little more than a funnel-like depression (Fig. 181). At first they often open directly on to the external surface of the embryo, but become carried inwards with further growth. Two or three pairs make their appearance and, in cases where a larger number is present, the additional tubes arise as diverticula of the primary formations.

The Nervous System.—The beginnings of the central nervous system appear as a pair of longitudinal *neural ridges* of the ectoderm of the germ-band, about the time when the latter becomes segmented. They commence at the sides of the stomodæum, and continue backwards until they unite behind the proctodæum. These ridges are separated by a median furrow—the *primitive* or *neural groove* (182, 189). A chain of cells forming the *median cord* is separated from the ectoderm lining the neural groove. The ectoderm cells forming the neural ridges become segregated into two layers,—an outer thin layer of *dermatoblasts* which forms the ventral body-wall and an inner layer of *neuroblasts* which forms the nervous tissue (Fig. 176). When the embryonic appendages commence to appear the neural ridges become segmented into definite swellings at the bases of the former, and each pair of these swellings constitutes a *neuromere*. The intrasegmental portions of the median cord and neural ridges give rise to the definitive ganglia, while the intersegmental portions of the ridges form the connectives.

In the cephalic region the neural ridges expand into broad *procephalic lobes*, forming the future supra-œsophageal ganglion, and they become divided into three neuromeres corresponding with the three primary cephalic segments. These neuromeres are known respectively as the *proto-*, *deuto-* and *tritocerebrum* (vide also p. 62): since the first two lie in front of the stomodæum, they are pre-oral in position, while the tritocerebrum is post-oral since the commissure uniting its two halves (ganglia) passes below the stomodæum. The *optic lobes* differ in their method of formation in different insects: thus in Orthoptera they are derived from neuroblasts and in Hymenoptera as infoldings of the superficial ectoderm.

The neuromeres of the first three protocormic segments fuse to form the sub-œsophageal ganglion, while the remaining neuromeres constitute the ganglia of the ventral nerve cord. These latter are nine to eleven in number and subsequently undergo varying degrees of fusion in different insects.

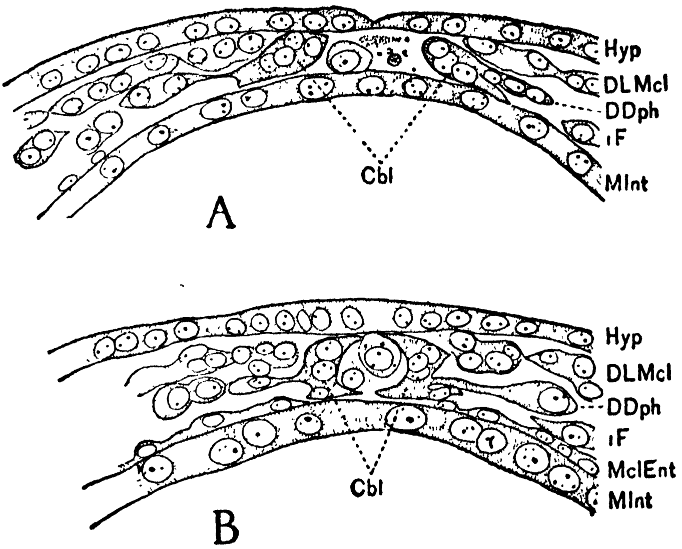

Fig. 188.—Transverse Sections of Dorsal Region of 4th Trunk Segment of late Embryo of Hive Bee × 600.

Cb, cardioblasts; *DDph*, dorsal diaphragm; *DLMcl*, dorsal longitudinal muscles; *Hyp*, hypodermis; *IF*, fat-body; *MInt*, mid-intestine and its muscles *MclEnt*. *After* Nelson, 1915.

The frontal ganglion and the remainder of the stomatogastric system develop as invaginations of the dorsal ectoderm of the stomodæum.

The Tracheal System.—Shortly after the appearance of the neuromeres the tracheæ appear as ectodermal invaginations lying just outside the bases of the appendages (Figs. 181, 191). As a rule, eleven pairs are developed, and they occur on the last two thoracic and first nine abdominal segments. In *Leptinotarsa* Wheeler has found indistinct invaginations also on the 10th and 11th abdominal segments: in *Apis* there are no invaginations beyond the 8th abdominal segment. Each invagination gives rise to a T-shaped horizontal outgrowth, which extends longitudinally until it meets and fuses with those of the segment in front and behind, thus forming the main longitudinal trunks. The mouths of the original invaginations contract and form the spiracles. In *Apis* there is also a pair of invaginations on the 2nd maxillary segment which form the anterior prolongations of the main tracheal trunks and subsequently close. After the main tracheal trunks are laid down branches therefrom extend inwards and, at the ends of the finer vessels, certain cells separate from the tracheal epithelium and grow out in a stellate form towards the tissues. It is in these cells that the tracheoles develop as fine intracellular tubes: where the tracheoles invade the cells of different organs they are apparently formed by branches of the tracheal cells directly penetrating the cytoplasm.

The Salivary Glands.—These appear as a pair of ectodermal ingrowths of the 2nd maxillary segment (Fig. 182). As they increase in depth their apertures approximate, and become drawn into the mouth where they finally open by a median pore. Carriere (1890) regards the salivary glands as modified tracheæ, and their original invaginations as representing the missing spiracles of the prothoracic segment which have migrated forwards.

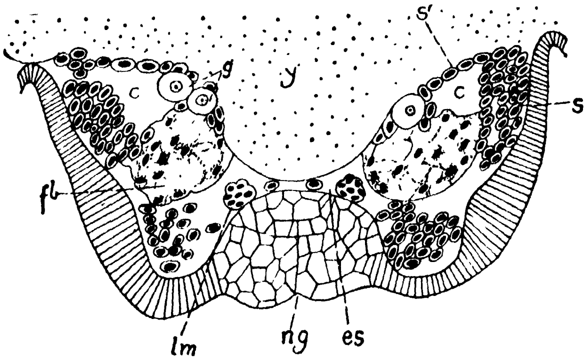

FIG. 189.—TRANSVERSE SECTION OF THE ABDOMEN OF THE EMBRYO OF *PHYLLODROMIA GERMANICA.*

For lettering, vide Fig. 191.

The Body-wall.—The body-wall is directly derived from the superficial ectoderm, and the essential parts of the organs of special sense are formed from the same layer.

The Body-cavity and Dorsal Vessel.—The permanent body-cavity commences as a space—the *epineural sinus*—which is mainly produced by the separation of the yolk from the embryo, over the region of the ventral nerve cord (Fig. 189). The process of separation extends laterally, and the walls of the cœlom sacs are stated to break through in such a manner that their cavities become confluent, both with one another and with the epineural sinus. The common cavity thus formed extends upwards along with the mesoderm, on either side, until the formation of the body-cavity is completed. The upward migration of the mesoderm carries the cardioblasts with it: the latter subsequently meet along the dorsal line of the embryo, and arrange themselves in the form of a tube, which is the rudiment of the heart. A single layer of cells unites the cardioblasts to the somatic mesoderm on either side, and eventually gives rise to the dorsal diaphragm (Figs. 188, 190). The aorta is formed by the union in the mid-dorsal line of the two cœlom sacs of the tritocerebral segment (*Donacia*), or of the deuto-cerebral segment (*Forficula, Apis*): by its backward extension the developing aorta comes to unite with the heart.

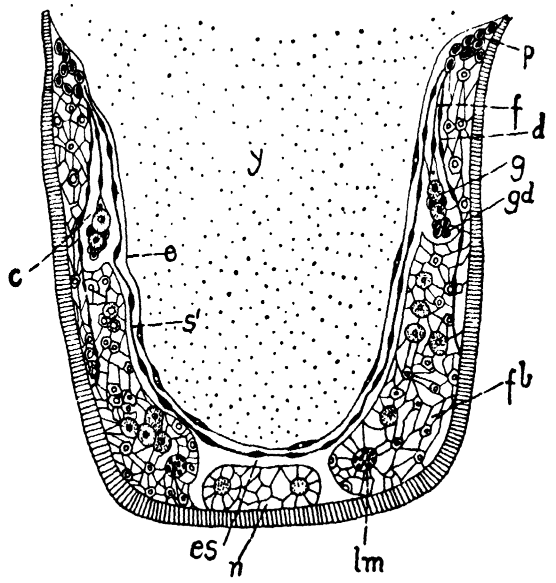

FIG. 190.—TRANSVERSE SECTION OF THE ABDOMEN OF THE EMBRYO OF *PHYLLODROMIA GERMANICA* WHERE THE GERM-BAND IS BEGINNING TO GROW AROUND THE YOLK.

For lettering, vide Fig. 191.

The Reproductive System.—The primitive germ cells in some insects, including *Donacia, Chironomus* and *Miastor,* are derived from special "pole cells" situated at the posterior end of the egg. In some cases these have been traced from a single original cell, distinguishable at an early stage of the cleavage (vide Hegner, 1914). Among other insects the primitive germ cells are believed to be derived from the mesoderm, but it is probable that they are likewise segregated at a very early stage, only are not capable of being definitely identified until later. In any event they migrate to the splanchnic mesoblast, coming to lie in the walls of the cœlom sacs—in the case of *Phyllodromia* in those of the 2nd to 7th abdominal segments. The germ cells become surrounded by mesoderm, which forms the *genital ridges*, and the latter fuse into a cell-strand lying on each side of the dorsal wall of the cœlom. The primitive germ cells give rise to the sex cells, while the enveloping mesoderm produces all other parts of the gonads and their primitive ducts. At an early stage a sheet of cells, the *filament plate*, is differentiated, and connects the apex of the genital rudiment with the heart rudiment of the same side of the body. With the migration of the heart rudiments towards the mid-dorsal line, the genital rudiments follow. Their primitive metamerism becomes lost, and it is only in later embryonic stages that sexual differences can be recognized. In the female the filament plate divides into eight strands or terminal threads, and these are connected with eight divisions of the ovary which represent the ovarioles. The undivided basal portion of the genital rudiment gives rise to the efferent duct of its side. The studies of Wheeler and Heymons on Orthoptera and Dermaptera show that the gonoducts of the two sexes are homodynamous rather than homologous structures, and each duct exhibits a primitive metamerism with original openings on the 7th and 10th abdominal segments (Fig. 192). In the

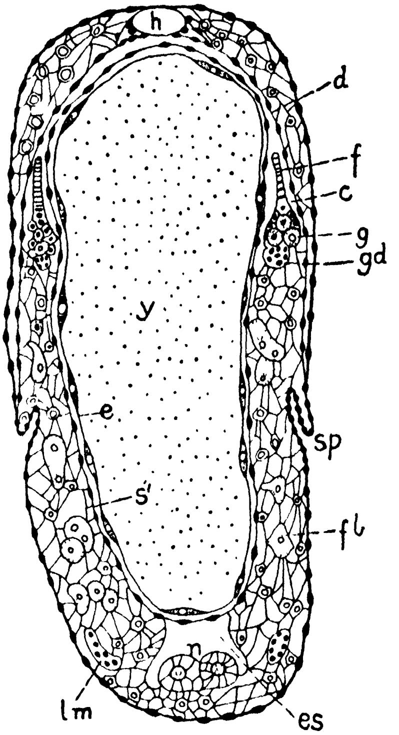

FIG. 191.—TRANSVERSE SECTION OF THE ABDOMEN OF THE EMBRYO OF *PHYLLODROMIA GERMANICA*, AFTER THE YOLK HAS BECOME ENCLOSED BY THE GERM-BAND.

c, cœlom; *d*, dorsal diaphragm; *e*, endoderm; *es*, epineural sinus; *f*, filament plate; *fb*, fat-body; *g*, genital cells; *gd*, rudiment of genital duct; *h*, heart; *lm*, ventral longitudinal muscles; *n*, rudiment of nerve-cord; *ng*, neural groove; *p*, cardioblasts; *s*, somatic mesoderm; s^1, splanchnic do.; *sp*, spiracle. This and Figs. 189, 190 *after* Heymons (with different lettering).

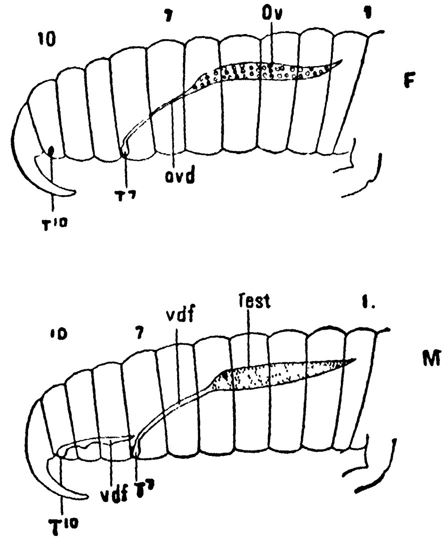

FIG. 192.—DEVELOPMENT OF GENITAL DUCTS OF EMBRYO *PERIPLANETA*.

F, female. M, male. 1, 7, 10, abdominal segments; *ov*, ovary; *Test*, testis; T^7, T^{10}, terminal ampullæ; *ovd*, oviduct *vdf*, vas deferens. From Henneguy, *after* Heymons.

Blattidæ and in *Gryllus* the primitive sexual openings in the female are those on the 7th segment and in the male they are those on the 10th segment. In each sex traces of an original hermaphroditism may be exhibited in the retention of vestiges of a condition of the gonoducts which belongs to the opposite sex. In *Forficula* the openings of both sexes are on the 10th segment, with vestiges of a former opening on the 7th segment in the female.

Except in rare instances (vide p. 153), the paired mesodermal ducts acquire connection with a median ectodermal invagination. The latter forms the ejaculatory duct in the male, and the vagina and uterus in the female together with their appendices.

Sequence of the Developmental Stages.—Data concerning the rate of development, and the time taken to arrive at the principal stages, are given in great detail by Heider for *Hydrophilus* and by Nelson for *Apis*. Since the data for *Hydrophilus* concern a more generalized type they are quoted here. Heider divides the developmental period into three phases, occupying altogether 11 days, and the most important facts may be summarized as follows.

1ST PHASE

1st Day.	Blastoderm completely formed.
2nd Day.	Metamerization of the germ band ; formation of amniotic folds, procephalic lobes, and middle plate.
3rd Day.	Appearance of neural groove and antennæ ; closure of amniotic folds.

2ND PHASE

4th Day.	Appearance of buccal and trunk appendages together with the stomodæum, which is followed by the proctodæum ; appearance of tracheal invaginations.
5th Day.	Elongation of appendages ; mouths of tracheal invaginations reduced to rounded orifices representing the spiracles.
7th Day.	Elongation of neural groove ; embryonic membranes rupture, exposing the embryo.

During this phase the separation of the endoderm from the mesoderm takes place and the rudiments of the mid-intestine are formed : the mesoblastic somites and body-cavity appear, and yolk cleavage occurs.

3RD PHASE

End of 7th Day.	Appearance of dorsal organ.
8th Day.	Dorsal organ completely formed.
9th Day.	Pigmentation of the eyes.
10th Day.	Eyes more pigmented ; main tracheal trunks visible.
11th Day.	Embryo becomes strongly pigmented and exhibits movements beneath the chorion.
12th Day.	Eclosion of the larva.

This phase is one of histological differentiation and no new permanent organs are developed.

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POSTEMBRYONIC DEVELOPMENT

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A. Metamorphosis

ECLOSION from the Egg.—The process of hatching or eclosion from the egg varies greatly in different groups. Some insects (e.g. caterpillars) simply eat their way through the embryonic membranes and chorion, while others rupture the chorion by body movements. In the Odonata a peculiar pulsating organ, or cephalic heart, exerts pressure against the egg shell and forces up a caplike operculum, thereby providing for the exit of the insect. Among Orthoptera the cervical ampulla performs a similar function, which is aided by convulsive movements of the body. Many insects have special *hatching spines* or egg-bursters. In *Leptinotarsa* there are three pairs of these spines on the body (Wheeler): in Aphaniptera there is a single spine on the head, and in the Pentatomidæ a T-shaped cephalic denticle. Among Anoplura and some Hemiptera the hatching spines are on the embryonic cuticle which is shed at the time of eclosion. In various other insects they are outgrowths from the cuticle of the first instar larva, or nymph, and consequently persist until ecdysis. The force employed in effecting eclosion appears to be muscular activity and Sikes and Wigglesworth (1931) claim that this action increases the osmotic pressure of the tissue fluids, and thereby causes absorption of fluid from the tracheæ. This process allows of air passing into the tracheæ until the respiratory system is filled. In cases where the tracheal system is closed the filling of the tubes is explained on the basis that gases in solution are liberated by the increase of osmotic pressure, already referred to.

✓**Instar and Stadium.**—Every insect during its growth sheds its skin one or more times, this process being known as a moult or *ecdysis*, the cast skin being termed the *exuviæ*. The intervals between the ecdyses are known as stages or *stadia*, and the form assumed by an insect during a particular stadium is termed an *instar*. When an insect issues from the egg it is said to be in its first instar: at the end of this stadium the first ecdysis occurs and the insect then assumes its second instar, and so on. The final instar is the fully mature form which is known as the adult or *imago*.

Metamorphosis.—One of the most characteristic features of insects is the fact that they are almost always hatched in a condition morphologically different from that assumed in the imago. In order to reach the latter instar they consequently have to pass through changes of form which are collectively termed *metamorphosis*.

Some insects emerge from the egg in a form resembling the imago and, therefore, pass through no metamorphosis: such insects are described as *Ametabola*. The Apterygota are usually regarded as being ametabolous, but in some cases a slight metamorphosis is present. Ametabolous forms also occur among apterous representatives of the Pterygota, whose transformations have become reduced to such a degree of insignificance that they no longer merit the term metamorphosis. Such forms have consequently acquired a secondary ametabolous growth and examples of this kind are found in the Phasmidæ, Anoplura, in the workers of the Isoptera and in female Embioptera.

The majority of insects pass through a metamorphosis and, in contradistinction to the primitively ametabolous species, are termed *Metabola.* In the strict zoological sense the immature forms of animals which undergo metamorphosis are called larvæ. Among insects it is customary and convenient to distinguish two types of immature individuals, viz., *nymphs* and *larvæ.*

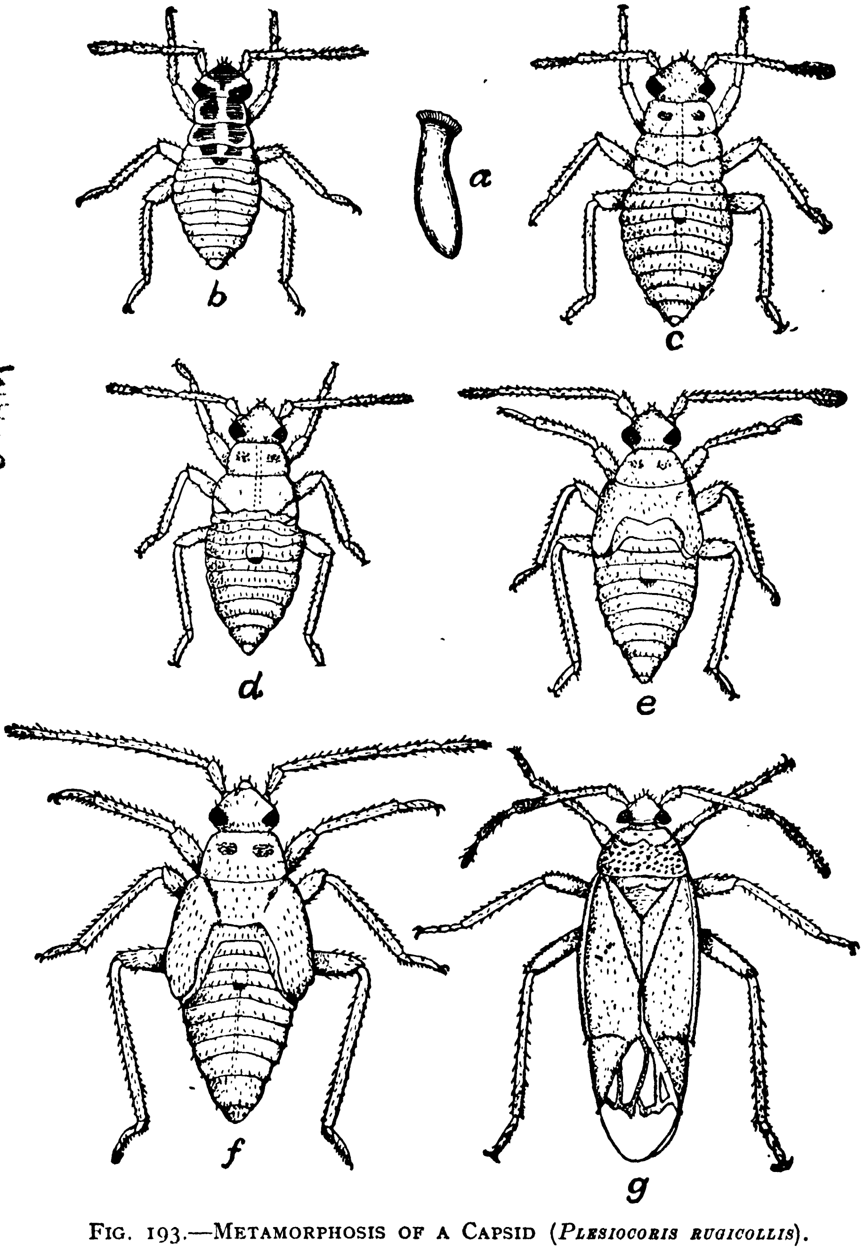

FIG. 193.—METAMORPHOSIS OF A CAPSID (*PLESIOCORIS RUGICOLLIS*).

a, egg ; *b-f*, nymphal instars (wing-rudiments minute in *d*, larger in *e* and *f*) × 20; *g*, imago × 8. From Carpenter, *after* Petheridge and Husain.

A *nymph* may be defined as a young insect which quits the egg in a relatively advanced stage of morphological development, and mainly differs from the imago in that the wings and genitalia are only present in an incompletely developed condition. The mouth-parts exhibit the same general type of construction as in the adult, while the compound eyes suffer no arrestation of development and are functional. The growth from the nymph to the imago is a simple one and is unaccompanied by a pupal instar.

A *larva* may be defined as a young insect which quits the egg in an early stage of morphological development, and differs fundamentally in form from the adult. The mouth-parts usually differ greatly in construction from those of the adult and compound eyes, with scarcely any exceptions, are either wanting or non-functional. The growth from the larva to the imago is by means of a complex metamorphosis accompanied by a pupal instar.

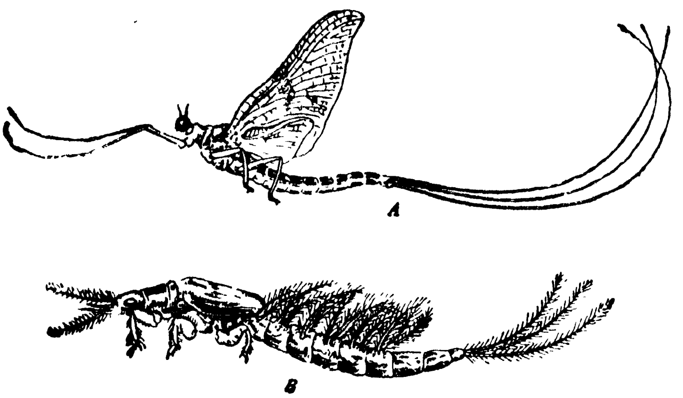

FIG. 194. METAMORPHOSIS OF *EPHEMERA*.
A, male imago. B, nymph. From Comstock *after* Needham.

Types of Metamorphosis.—The orders of insects exhibiting metamorphosis are often divided into two main groups: (1) Hemimetabola and (2) Holometabola.

1. HEMIMETABOLA.—This term is applied to members of the lower orders (or Exopterygota: p. 214) which pass through a simple metamorphosis often described as *direct* or *incomplete*. A pupal stage is wanting, and the immature insects are referred to as nymphs.

The degree of metamorphosis which prevails varies in different orders of Hemimetabola. In many cases the young resemble the adults in general form and mode of life (Fig. 193). Postembryonic development is consequently one of gradual growth, unaccompanied by any striking morphological change. The distinctive feature of this type of metamorphosis is the acquisition of wings and genitalia. Among the Plecoptera, Odonata and Ephemeroptera (Fig. 194) the nymphs differ from the adults in possessing provisional organs. Since they live in water, while the imagines are aerial, these differences are of an adaptive nature and chiefly concern the respiratory and locomotory organs. In the Thysanoptera, Aleurodidæ and male Coccidæ attempts, as it were, towards holometabolism are evident in that an incipient pupal instar has become intercalated in the ontogeny.

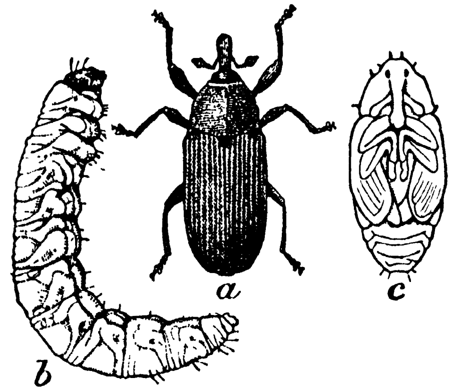

FIG. 195.—METAMORPHOSIS OF A WEEVIL (*TRICHOBARIS TRINOTATA*).
a, imago; *b*, larva; *c*, pupa. *After* Chittenden, *U.S. Dept. Agric. Ent. Bull.* 33 (n.s.).

2. HOLOMETABOLA.—This term is given to members of the higher orders (or Endopterygota, p. 214) which pass through a complex metamorphosis: the young are larvæ and the imago is preceded by a pupal instar (Fig. 195). Such a type of metamorphosis is often referred to as *indirect* or *complete.*

Types of Insect Larvæ.—In discussing the larval forms of insects it is necessary, in the first instance, to consider the progressive development of metamerism in the embryo. As a rule segmentation commences at the anterior extremity, and extends backwards, although there are modifications and exceptions to this sequence. Berlese (1913) recognizes three successive embryonic phases in the development of insects, these phases being based primarily upon the condition of the metamerism, viz., *protopod, polypod,* and *oligopod* (Fig. 196).

Parasitic hymenoptera

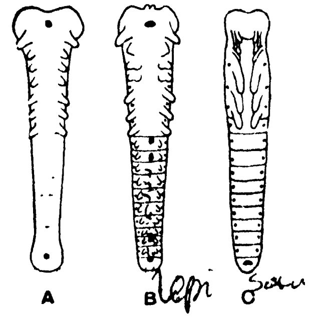

FIG. 196.—EMBRYONIC PHASES.

A, protopod. B, polypod. C, oligopod. *After* Berlese, *Redia*, 9.

In the *protopod phase* metamerism is incomplete, the abdomen being imperfectly differentiated and, if segmented, its metameres have not as yet acquired appendages. The digestive and nervous systems are in a rudimentary condition and the tracheal invaginations are undeveloped.

In the *polypod phase* the abdomen has acquired its complete segmentation and full number of appendages. The internal organs are further differentiated and tracheal invaginations are formed.

In the *oligopod phase* the embryo has reached an advanced condition: the thoracic limbs have increased in size, and the evanescent abdominal appendages have disappeared. At the end of this phase the nymphs of insects with incomplete metamorphosis issue from the egg.

In general, insect larvæ represent an arrestation in one or other of these phases when eclosion from the egg takes place. Larvæ, therefore, generally issue from the egg at an earlier ontogenetic stage than nymphs.

The various types of insect larvæ may be conveniently classified with reference to the embryonic phases they most closely resemble in basic characters.

1. PROTOPOD LARVÆ.—This type is found in the primary larvæ of certain parasitic Hymenoptera. The eggs of such species contain but little yolk and the larvæ are compelled, as it were, to emerge while still in an early embryonic phase. Their survival is rendered possible from the fact that they occur in the eggs, or in the bodies, of other insects where they develop immersed in a highly nutritive medium. Protopod larvæ are characteristic of the Platygasteridæ (Fig. 197) where, in *P. herrickii*, the larva is little more than a prematurely hatched embryo, devoid of segmentation in the abdomen and with rudimentary and cephalic and thoracic appendages. The nervous and respiratory systems are as yet undeveloped, and the digestive organs are still largely in an embryonic phase. In the cyclopoid primary larva of other species of *Platygaster* (Fig. 198) and of *Synopeas* there is a greatly developed cephalothorax,

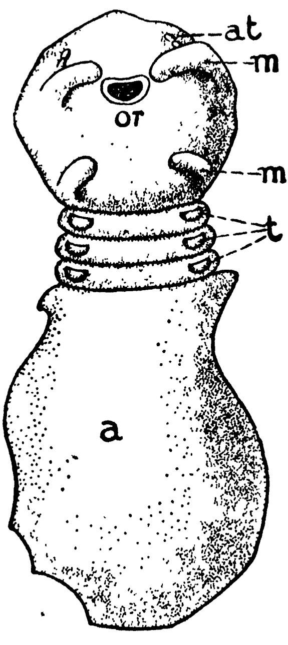

FIG. 197.—PROTOPOD 1ST INSTAR LARVA OF *PLATYGASTER HERRICKII.*

a, abdomen; *at*, antenna; *m*, mandible; *m*₁, maxilla, *or*, oral aperture; *t*, thoracic appendages. *After* Kulagin.

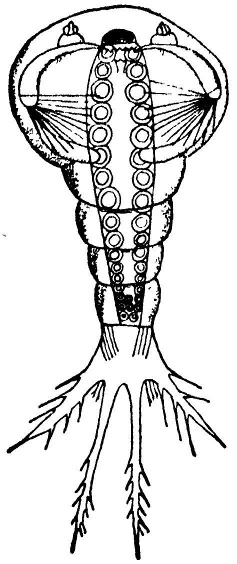

Fig. 198.—First larval Instar (Protopod) of *Platygaster*. *After* Ganin.

powerful jaws and elaborate caudal outgrowths. The so-called eucoiliform larva of the Figitidæ is also a specialized protopod type with greatly developed thoracic appendages.

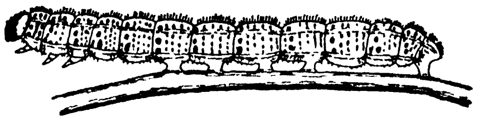

Fig. 199.—Eruciform (Polypod) Larva of *Pieris brassicæ*.

2. POLYPOD LARVÆ.—Typical examples of this type (Fig. 199) are seen in the so-called *eruciform larvæ* of Lepidoptera, of sawflies and of scorpion flies. Their essential features are the retention of abdominal limbs and the presence of a peripneustic tracheal system. The antennæ and thoracic legs are but little developed and such larvæ are relatively inactive, living in proximity to their food. The existence of a presumed polypod instar among endoparasitic hymenopterous larvæ is a recent discovery. It occurs in the Figitidæ where there are ten pairs of abdominal appendages (James): in *Ibalia* where there are twelve pairs (Chrystal) and in the Proctotrypid *Phænoserphus* where there are eight pairs of such organs (Eastham). In the Figitidæ the polypod instar follows the protopod stage but, in the other examples, the latter phase is presumably passed through in the egg. Owing to an endoparasitic mode of life the spiracles are undeveloped in these examples.

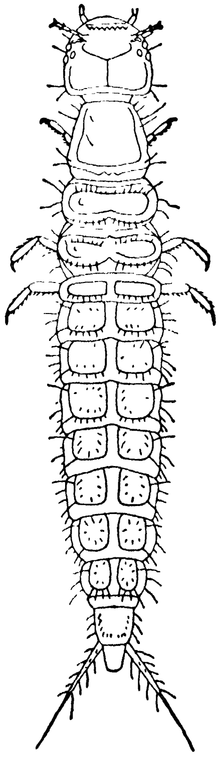

Fig. 200.—Campodeiform (Oligopod) Larva of a Staphylinid (*Philonthus nitidus*). *After* Schiödte.

3. OLIGOPOD LARVÆ.—The oligopod type is most typically represented in the campodeiform (or thysanuriform) larvæ of many Coleoptera. Such larvæ are hatched in a form bearing a general resemblance to the adults of *Campodea*, and other Thysanura, and are regarded as representing a thysanuran stage in the ontogeny of the species to which they belong (Fig. 200). They are active predators seeking out their prey and have well-developed feeding, locomotory and sensory organs, and an armoured integument. This type of larva, unlike the Thysanura, never bears abdominal appendages and Berlese regards it as representing the oligopod phase, and therefore a post-thysanuran stage, in development. Nymphs closely resemble campodeiform larvæ but represent a more advanced condition of the oligopod phase, having, for example, compound eyes and often dorsal ocelli as in the adults. Primitive examples of campodeiform larvæ are found in the Adephaga, Staphylinidæ, the first instar of *Mantispa*, in the Meloidæ and Strepsiptera: they are also very characteristic of Neuroptera. Among Coleoptera there exist numerous larval types, some of which retain the armoured integument and reduced facies of the campodeiform larva (many Diversicornia and Heteromera). Others exhibit a marked approach to the eruciform

type, in that they are fleshy and unarmoured (Lamellicornia). Others, again, are more degenerate with greatly reduced locomotory and sensory organs, and lead an inactive life amidst an ample supply of food (Elateridæ, Cerambycidæ, Bruchidæ). They are obviously specialized oligopod forms derived by modification from the campodeiform type. This conclusion is borne out by species undergoing hypermetamorphosis (e.g. Meloidæ, Rhipiphoridæ, *Aleochara*, etc.), where the active campodeiform first instar is followed by one or more instars showing degenerate oligopod facies (Fig. 201).

4. APODOUS LARVÆ.—In this type the trunk appendages are completely suppressed and, in the vast majority of cases, it is derived from the oligopod phase. Among Coleoptera the apodous condition occurs in several families and, in the Bruchidæ, it is preceded by a degenerate oligopod instar, while in the Curculionidæ the last rudiments of thoracic limbs are retained as sensory protuberances in *Phytonomus* (Pérez, 1911). In the Hymenoptera the apodous condition occurs in all larvæ of the Apocrita—traces of an oligopod stage have been detected in *Polysphincta* and certain other of the Ichneumonoidea. In the Symphyta a long series of transitional forms occur from typical polypod types to oligopod forms, finally culminating in the apodous larva of *Oryssus*.

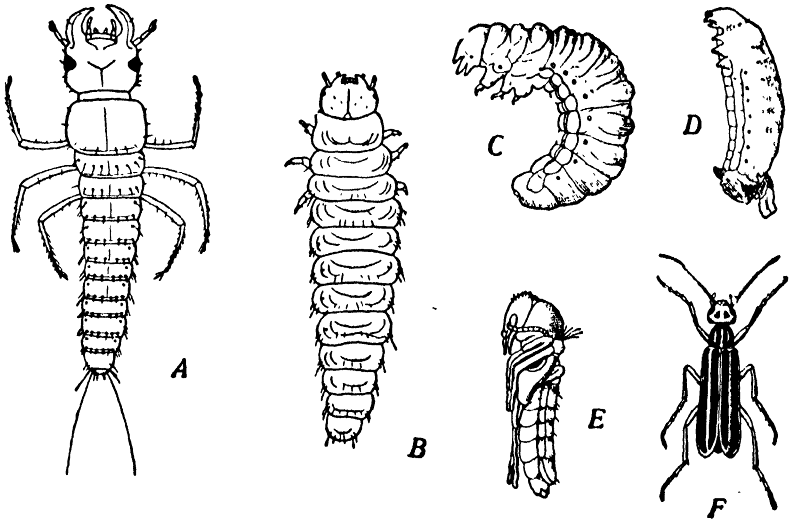

FIG. 201.—HYPERMETAMORPHOSIS OF *EPICAUTA*.

A, triungulin; B, caraboid second instar; C, ultimate form of second instar; D, coarctate larva; E, pupa; F, imago. All refer to *E. vittata* except E, which is *cinerea* (F nat. size, others enlarged). From Folsom's Entomology *after* Riley.

In Diptera the larvæ are always apodous but bear three pairs of sensory papillæ in direct relation with the developing imaginal leg-buds—thus they occupy the positions of ancestral thoracic limbs of which they are the transformed vestiges (Keilin, 1915). Dipterous larvæ are, therefore, to be regarded as highly specialized derivatives of the oligopod type. A clearly defined polypod phase in this order has become obliterated from all stages in the ontogeny.

It needs to be remembered that not every larva hatches in a condition exactly comparable with one or other of the embryonic phases alluded to. Intermediates are numerous and, furthermore, the ancestral forms of larvæ are liable to be masked by superimposed adaptive secondary modifications.

Hypermetamorphosis.—When an insect in its development passes through two or more markedly different larval instars it is said to undergo *hypermetamorphosis* (Fig. 201). This phenomenon is accompanied as a rule by a marked change in larval life. In the majority of instances of hypermetamorphosis the first larval instar is campodeiform. During this stage it seeks out its future pabulum and having discovered it undergoes, in its subsequent instars, morphological transformations which adapt it to the changed mode of life.

Since various examples of hypermetamorphosis are described under the several families concerned they need not be discussed here, and only the principal instances are enumerated below.

NEUROPTERA. *Mantispa.*

COLEOPTERA. Carabidæ (*Lebia scapularis*). Staphylinidæ (*Aleochara* spp.) Meloidæ. Rhipiphoridæ.

STREPSIPTERA. All species.

DIPTERA. Bombyliidæ. Cyrtidæ. Nemestrinidæ. Some Tachinidæ.

HYMENOPTERA. In all the chief groups of Parasitica.

HEMIPTERA. Coccidæ—*Margarodes* and allies.

Ecdysis.—The more or less rigid integument is ill adapted for accommodating itself to the increase in size of an insect that is consequent upon growth, and is therefore periodically shed. During each act of ecdysis not only the general cuticle investing the body and its appendages is cast off, but also the lining or intima of the tracheæ, fore- and hind-intestine, glands, etc. All these parts, together with hairs, scales, and similar structures, are renewed by the hypodermal cells underlying them.

The actual process of ecdysis has been described by Tower (1906) in Coleoptera, Wachter (1930) in Lepidoptera, Wigglesworth (1933) in Hemiptera and by others. It first becomes evident by the swelling of the hypodermis whose cells undergo mitosis and multiply. During this phase the hypodermis becomes separated from the cuticle and the exuvial glands (p. 148) become actively functional. The hypodermis first lays down a new epicuticula over its entire surface and the exocuticula is formed beneath soon afterwards. These two cuticular layers participate in the formation of new hairs, scales, etc., which replace the old. Such organs lie compressed beneath the old cuticle and very possibly exercise a function in loosening it. Verhoeff contends that many of the spinous processes of certain pupæ serve a more important function in loosening the old larval skin, than in aiding pupal locomotion. The ducts of the exuvial glands extend through the new cuticle and the moulting fluid, that is discharged, dissolves much of the old skin so that it becomes greatly reduced in thickness. What is left of the original cuticle is consequently separated from the new cuticle by a thin film of fluid. The old skin becomes completely detached from the new and eventually ruptures—usually along the back of the head and thorax. The anterior extremity of the insect is protruded through the fracture thus formed, and the exuviæ is worked backwards towards the caudal end of the body where it is cast off. The moulting fluid corrodes and softens the old skin rendering it more flexible. When first cast off it is possible to extend the old skin to its former length, but the moulting fluid which bathes it quickly hardens and the skin soon becomes rigid. In cases where the cuticle is of extreme tenuity, as in parasitic hymenopterous larvæ, the shrivelled skin often remains around the hindmost segments of the body; several of the superposed exuviæ are sometimes observable in this condition, and are recognizable by the remains of the head-capsules of previous instars.

After ecdysis the exocuticula hardens, rapidly deepening in colour, while the new endocuticula becomes formed beneath it.

A very wide range of variation is exhibited with regard to the number of ecdyses undergone by different insects. Thus according to Grassi there is only a single fragmentary ecdysis in *Campodea* and *Japyx*, while the may-fly *Chlœon* was found by Lubbock to moult twenty-three times. Almost every transitional condition is met with between these two extremes, but, as a general rule, the number of ecdyses is five or six. In the Diptera Cyclorrhapha and Neuroptera Planipennia, two ecdyses only are very constant while among Lepidoptera the number is extremely variable : in some species it may be as high as nine and in others as low as three. It may also vary within the limits of a single species as in *Arctia caia*. The factors determining the number of ecdyses need investigation and it is at present impossible to judge how far they are phylogenetic in significance, and how far they are an expression of internal physiological processes in the species concerned.

Some insects undergo ecdysis almost immediately after leaving the egg. The Collembola are stated to be exceptional in that ecdyses occur after attaining sexual maturity and the Ephemeroptera alone exhibit the unusual feature of an ecdysis taking place after the insect has acquired functional wings. With these exceptions ecdysis is confined to the pre-imaginal instars.

Dyar's Law.—Dyar (1890) has shown from observations on the larval instars of twenty-eight species of Lepidoptera that the head-width follows a regular geometrical progression in successive instars. Since the head is not subject to growth during a stadium it is possible, by means of accurate measurements, to determine whether an ecdysis has been overlooked or not during life-history studies. In the example below the observed and calculated head-widths in mm. in the seven larval instars of *Halisidota harrisii* Walsh are given. By dividing each observed number in the series by the one which precedes it a ratio of increase in each instar is found ; the average of these ratios for the example given is 1·44.

Calculated Widths			*Observed Widths.*	
Width observed in 1st instar			·4	·4
Calculated width in 2nd „	(·4 × 1·44) =	·57	·6	·6
„ „ „ 3rd „	(·57 × 1·44) =	·82	·9	
„ „ „ 4th „	(·82 × 1·44) =	1·18	1·4	1·3
„ „ „ 5th „	(1·18 × 1·44) =	1·69	1·6	1·7
„ „ „ 6th „	(1·69 × 1·44) =	2·43	2·3	2·6
„ „ „ 7th „	(2·43 × 1·44) =	3·49	3·5	3·6

It will be noted that the approximation of the observed to the calculated measurements is sufficiently close to preclude the probability of an ecdysis having been overlooked. The " law " applies also to saw-fly larvæ and Collembola.

Growth.—The larval and nymphal periods are pre-eminently ones of growth. The rapidity with which this process takes place, and the great increase in size that accompanies it, are particularly evident in many holometabolous insects. Growth, however, is interrupted at each ecdysis, and just before that process occurs an appreciable fall in weight takes place. A comparison of the weight of a mature larva with that at the time of eclosion from the egg has been made in several species. Thus Trouvelot found that the silkworm *Telea polyphemus* when fully grown is 4,140 times its original weight. In the larva of the bee *Anthophora retusa* the corresponding increase is 1,020 times (Newport) ; in the larva of *Cossus cossus*, which lives for three years, it is 72,000 times (Lyonnet) ; in *Sphinx ligustri* 9,976 times (Newport) ; in the silkworm *Bombyx mori* the increase varies according to racial and other factors between about 9,100 times and 10,500 times.

The most complete data available concerning growth is in the case of the mulberry silkworm (vide *Rep. Imp. Sericult. Inst. Tokyo*, 1910). On hatching 100 larvæ were found to weigh ·038 grm., and their subsequent growth, given in tabular form, is as follows. (The figures are per 100 larvæ.)

Instar.	Live-weight at maximum point of growth.	Increase of live weight over that of newly hatched larvæ.	Average length.	Increase in length over that of newly hatched larvæ.
	grm.	times	cm.	times
1st	·54	12·75	·575	1·90
2nd	2·65	68.31	1.152	3·80
3rd	14·88	343·28	2.048	7·36
4th	80.22	1818.22	4·279	14·12
5th	356·44	9126·21	7·222	23·80

The relation of the weight of 100 larvæ to the quantity of food eaten and digested is as follows (average of three races):—

Instar.	No. of days in instar.	Weight at end of instar.	Dry weight of food eaten.	Weight of excreta.	Weight of digested food.	Digested food per 100 grm. of food.
	d. h.	grm.	grm.	grm.	grm.	grm.
1st	6. 1	·52	·30	·15	·15	50·25
2nd	5· 3	2.67	1·32	·59	·72	54·73
3rd	5· 6	12·78	6.53	3·69	2·80	42·91
4th	7· 1	56·86	29·47	18·96	10·50	34·60
5th	7·10	256·64	190·36	129·41	60·27	31·78
Totals	30·21	—	227·99	153·53	74·46	32·74

According to Hiratsuka (1920) the data vary according to the sex of the larvæ The amount of fresh leaves consumed by 100 larvæ (both sexes) in the 1st instar was found to be 1·48 grm. and in the 5th instar the same number of male larvæ consumed 986·33 grm. and of female larvæ 1182·20 grm. The greatest activity in tissue-building is in the 1st instar: at this period the live-weight increases threefold in 24 hours but afterwards the rate of growth gradually falls as age advances.

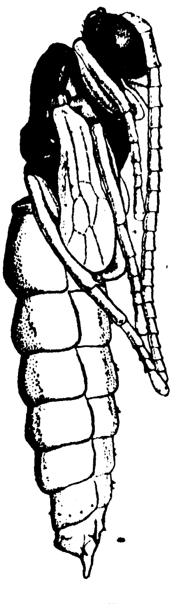

FIG. 202.— EXARATE OR FREE PUPA OF A HYMENOPTERON (ICHNEUMONIDÆ): LATERAL VIEW.

The Pupa.—The name "pupa" signifies "baby" and was given by Linnæus to the chrysalis of Lepidoptera on account of its resemblance to an infant which has been swathed or wrapped up as is customary among certain peoples. The term *pupa* is now used with reference to the resting inactive instar in all holometabolous insects. During this stage the insect is incapable of feeding and is quiescent. It is to be regarded as an acquired transitional phase during which the larval body and its internal organs are remodelled to the extent necessary to adapt them to the requirements of the future imago. Although normally motionless, many pupæ possess a limited capacity for locomotion which becomes evident towards the end of the stadium, when it facilitates the emergence of the perfect insect.

Three types of pupæ are generally recognized.

(1) THE EXARATE OR FREE PUPA (Fig. 202).—In this type the wings and legs are free from any secondary attachment to the body and such pupæ exhibit a greater capacity for movement than other types. Exarate pupæ are characteristic of all the lower Endopterygota, including the Neuroptera Mecoptera, Coleoptera, Trichoptera, and the Micropterygidæ among Lepidoptera: they are also found throughout the Hymenoptera.

(2) THE OBTECT PUPA (Fig. 203).—In this type the wings and legs are firmly soldered down to the body by the moulting fluid after the final larval ecdysis. Obtected pupæ are characteristic of Lepidoptera and are also found in the Diptera Orthorrhapha, and in the Staphylinidæ and Coccinellidæ among Coleoptera.

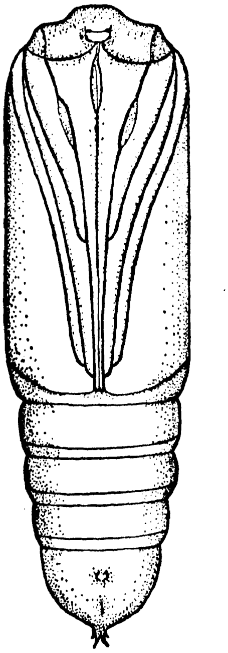

FIG. 203.—OBTECT PUPA OF A LEPIDOPTERON (NOCTUIDÆ): VENTRAL VIEW.

(3) THE COARCTATE PUPA (Fig. 204).—In the Diptera Cyclorrhapha the last larval skin is retained as a covering to the pupa, becoming hardened and completely separated from the insect which it encloses. This pupal covering or capsule is known as the *puparium*, and pupæ protected in this manner are termed coarctate. As a rule puparia are cylindrical or barrel-shaped and they betray no outward indication of the developing insect within.

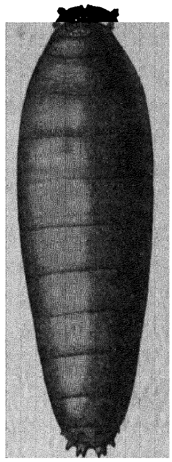

FIG. 204.—COARCTATE PUPA OF A DIPTERON (ANTHOMYIDAE): DORSAL VIEW.

Mention has been previously made of the locomotory capacity of pupæ. Among some Neuroptera including *Raphidia*, *Hemerobius* and *Chrysopa* the pupæ regain considerable activity before the final ecdysis and are able to crawl about. Those of certain of the Trichoptera exhibit adaptive modifications which enable them to swim to the surface of the water to allow of the exit of the imagines. In the Culicidæ and certain Chironomidæ the pupæ are active throughout the instar, and are capable of vigorous swimming by means of caudal movements. Movements of a less pronounced character are exhibited by many pupæ which occur in the soil, in wood or in stems. In cases of this kind they are commonly armed with spines or denticles which facilitate their movements towards the exterior, when the time for the emergence of the imagines approaches.

The Prepupa.—The existence of an instar between the last larval and the pupal stadia is sometimes overlooked. Near the end of the larval period the insect prepares itself for transformation into the pupa, usually constructing a cocoon, cell, or other form of protection. A brief period of quiescence then follows which marks the prepupal instar (Fig. 205). At this period the wings and appendages become everted from their sacs, and lie for the first time outside the body, where they are found beneath the old larval cuticle which still persists. The thorax becomes modified and other changes in the general form of the insect are assumed. In Hymenoptera, for example, it is at this period that the first abdominal segment

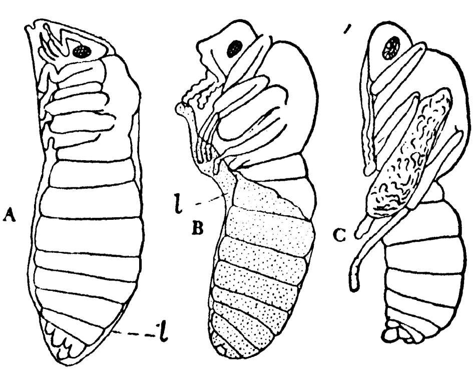

FIG. 205.—EXTERNAL CHANGES DURING PREPUPAL AND PUPAL INSTARS OF *FORMICA RUFA*.

A, prepupa; B, change into pupa; C, pupa; *l*, larval skin. *After* C. Pérez, 1902.

becomes amalgamated with the thorax. The old larval skin is ultimately cast off and after a short interval the more lengthy resting stadium of the pupa is entered upon. The prepupa represents a greatly abbreviated instar during which an ecdysis has been suppressed.

Pupal Protection.—During transformation into the pupa and throughout the latter instar insects are particularly vulnerable. Since at these periods they are provided with exceedingly limited powers of movement and no means of defence, special methods of protection are necessary. Most pupæ are concealed in one way or another from their enemies, and also from such adverse influences as excess of moisture, sudden marked variations of temperature, shock and other mechanical disturbance. Provision against such influences is usually made by the larva in its last instar. Many lepidopterous and coleopterous larvæ burrow beneath the ground and there construct earthen cells in which to pupate. The larger number of insects, however, construct cocoons which are special envelopes formed either of silk alone, or of extraneous material bound together by means of threads of that substance. Thus many wood-boring larvæ utilize chips, larvæ which transform in the ground select earth particles: many Arctiad larvæ use their body-hairs and Trichoptera use pebbles, vegetable fragments, etc., their larval cases functioning as cocoons. In these instances the substances are held together by means of a warp of silk and worked up to form cocoons. A large number of other insects, including some of the Neuroptera and Trichoptera, many Lepidoptera and Hymenoptera and the Aphaniptera, utilize silk alone in forming their cocoons. Great variations exist in the colour and nature of the silk and in the texture and form of the completed cocoons. The densest and most perfect types of cocoon are found in the Saturniidæ, while the other extreme is met with in the Papilionina, where the pupa may be suspended by its caudal extremity, which is hooked on to a small pad of silk representing the last vestige of a cocoon. Exposed pupæ of this type are commonly protectively coloured. Among the Tenthredinidæ cocoons of a parchment-like or shell-like consistency are frequent: in some cases the outer cocoon encloses an inner one of more delicate texture.

In the Diptera Cyclorrhapha a cocoon, with very rare exceptions, is wanting, and the hard puparium forms the sole protection to the pupa. A cocoon is also wanting in the Chalcidoidea.

Emergence from the Cocoon.—Many insects upon issuing from the pupa leave the case or cuticle of the latter behind, and gnaw their way through the wall of the cocoon by means of their mandibles. This is the prevalent mode of exit among Coleoptera and Hymenoptera. In other cases the pupa is provided with mandibles which perform this same function, as happens among the Neuroptera and Trichoptera and *Micropteryx.* In other examples the pupa ruptures the cocoon by means of a special cocoon-breaker which takes the form of a spine or spines on the head, or at the bases of the fore-wings: or the cocoon may be softened by a secretion exuded from the mouth of the imago. These and other methods of emergence are further dealt with under the order Lepidoptera.

Eclosion of the Imago.—As the time for the eclosion of the imago approaches the pupa noticeably darkens in colour. In some of the more transparent pupæ of the Papilionina the colours of the imago are distinctly observable a short period before its emergence. When the time for the latter arrives, the contained insect, by means of convulsive movements of its legs and body, succeeds in rupturing the pupal cuticle. A longitudinal fracture occurs down the back of the thorax, and there are often other fractures in the region of the legs and elsewhere. The insect withdraws its appendages from within those of the pupa and emerges completely formed except for the wings. It crawls up the nearest available support and there rests in such a position that the folded miniature wings are inclined downwards. By the influx of blood from the body, and pressure exerted upon that fluid by muscular action, the complete expansion of the wings is rapidly acquired (Fig. 206). During this preliminary phase drops of liquid (the *meconium*) are discharged from the anus: they represent the waste products of pupal metabolism, and in Lepidoptera are coloured with residual pigmentary matter which has not been utilized. A short period elapses after eclosion before the insect is able to make its trial flight. The time of emergence varies greatly in different species. In some Lepidoptera, for example, it occurs in early morning and in others towards evening: at such times they may sometimes be observed resting upon tree trunks, etc., awaiting their normal hours of activity. Among certain aquatic insects the imago is able to take to the wing almost immediately after eclosion.

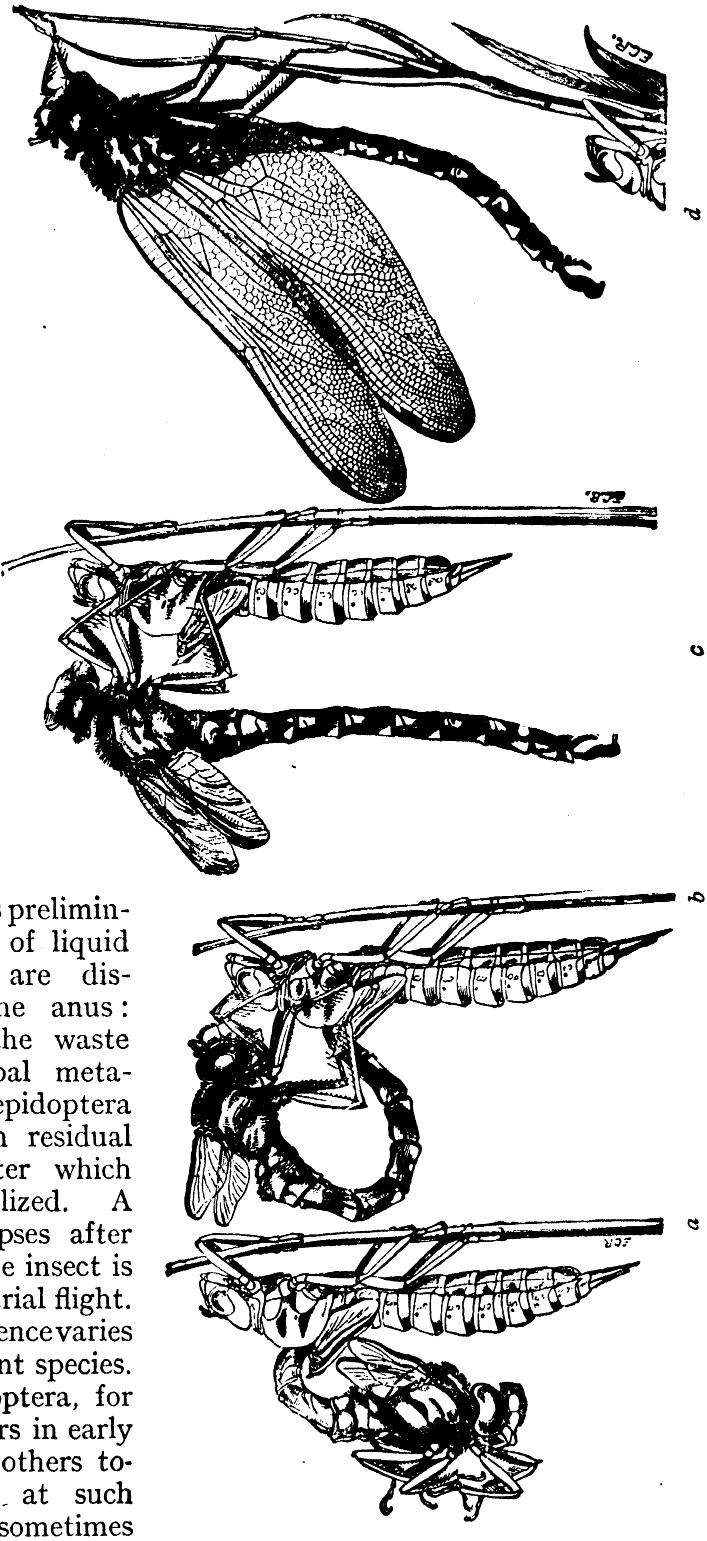

FIG. 206.—STAGES IN THE EMERGENCE OF A DRAGON-FLY (ÆSCHNA CYANEA.)

a–c, from the nymphal cuticle; *d*, fully-formed imago. *After* Latter, *Nat. Hist. of Common Animals.*

Origin of the Pupal Instar.—The pupal instar is to be regarded as a prolongation of the shorter period of inaction which frequently accompanies each ecdysis. Among the Isoptera one of these quiescent phases becomes a pronounced feature in the ontogeny of many of the species. Thus, in several species of *Termes* Bugnion has observed that the workers and soldiers pass through a period of hypnosis lasting seven or eight days, during which the transformation into the final instar is accomplished. While the insect is in this condition its head is downwardly flexed upon the thorax, while its antennæ and legs are directed backwards along the ventral surface. The quiescent phase is even more pronounced in *Rhinotermes taurus* (Fig. 207) and prefigures, as it were, the primitive type of exarate pupa. A similar phase has been noted during the final transformation into the winged form in other termites. The incipient pupa of the Thysanoptera is a definite and more lengthy resting phase which likewise precedes the appearance of the imago.

In the above instances, however, the wing-rudiments remain externally to the body throughout their growth. It is consequently evident that a further evolutionary stage has to be passed through, before the conditions of wing-growth which precede the true pupa of the Endopterygota are arrived at. Among the latter insects the wing-rudiments sink within the body from the beginning, and their outward appearance is postponed until after the last larval instar. A near approach to the endopterygote condition is afforded by the Aleyrodidæ and the males of the Coccidæ. An Aleyrodid, in its last larval instar, settles down upon a leaf and ceases to feed, while the cuticle separates from the body without actually being cast off. The wings are derived from internal buds which become everted and the insect, at this stage, is a quiescent nymph or rudimentary pupa which is protected by the persistent larval cuticle. The latter eventually dehisces to allow of the eclosion of the imago. In the males of the Coccidæ rudimentary prepupal and pupal instars are present. The wings, however, develop externally, but the adult limbs are new formations derived from imaginal buds. Some further observations on this subject are given under the families concerned.

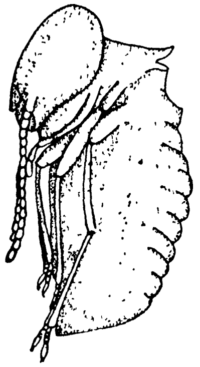

FIG. 207.—QUIESCENT NYMPHAL PHASE OF A TERMITE (*RHINOTERMES*).

After Holmgren, *Zool. Jahrb. Syst.*, 23.

The endopterygote condition is derived from the sinking in of the wing-buds with the result that their outward appearance becomes more and more delayed. The prepupal instar is to be regarded as a survival from exopterygote ancestors and it is noteworthy that occasional atavistic larvæ are found among Endopterygota (e.g. in *Tenebrio molitor*, etc.) in that they bear external wing-buds.

On a previous page it has been pointed out that insect larvæ are often hatched in an earlier stage of development than nymphs. In the former the imaginal wing-buds are internal and in the latter they are external. The nymphal period corresponds to the pupal stadium of the higher insects, the obvious difference being that the nymph is active and seeks its food while the pupa is quiescent and does not feed. If this comparison be correct it follows that several instars and ecdyses have been eliminated from the ontogeny during the pupal stadium, and that the latter consequently represents an example of abbreviation of development.

B. The Development of the Imago

The culminating feature of metamorphosis is the formation of the imago. The characteristic distinctions between hetero- and holometabolous insects with regard to the manner of development of the perfect insect have already been pointed out. In the Hemimetabola it is accomplished through a gradual series of external and internal changes and alterations of form, which may be traced back to simple growth during the nymphal instars. In the Holometabola the transformation from the larva to the imago is accomplished through the intercalation of a quiescent or pupal instar. Since the latter method of development involves complicated ontogenetic changes a more detailed consideration is necessary. These changes may be discussed under two headings—(1) the development of the external form of the imago and (2) the development of the internal organs.

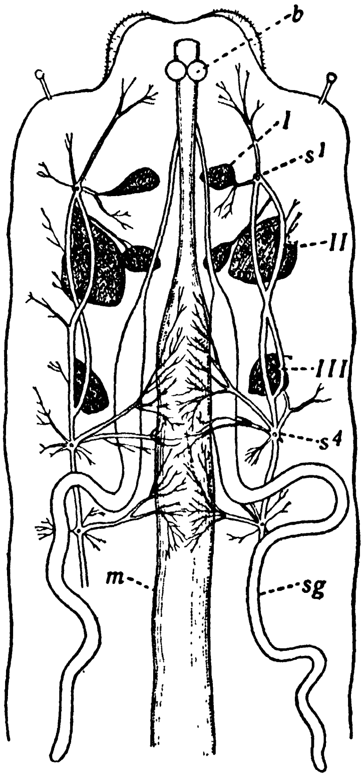

FIG. 208.—FULLY GROWN LARVA OF *PIERIS* DISSECTED FROM ABOVE SHOWING IMAGINAL BUDS.

b, brain; *m*, mid-intestine; s^1 prothoracic spiracle; s^4, 1st abdominal spiracle; *sg*, silk gland; I, prothoracic bud; II and III, buds of fore- and hind-wings. From Folsom's *Entomology*, *after* Gonin.

1. The Development of the External Form of the Imago.—The formation of the body and its appendages becomes evident in the larval period and attains completion during the pupa. The principal agents in the process are certain masses of formative cells variously known as *imaginal buds*, *imaginal discs* or *histoblasts* (Fig. 208). They arise as slight folds or thickenings of the hypodermis, and their cells exhibit the potentiality of embryonic tissue. On the inner aspect of the imaginal buds are found loose cell accumulations often referred to as mesenchyme. The origin of these cells has been much disputed, and it is believed by most authorities that they are derived from the embryonic mesoderm: by others it is maintained that they are formed by the delamination of the ectoderm of the imaginal buds.

The usual time of appearance of the imaginal buds is during the larval stadia, but in the higher Diptera they are already evident in the late embryo. These structures are present for each part of the body, including the appendages of the head, the wings, legs, genitalia, and the hypodermis of the abdomen. They usually appear as evaginations from previously developed hypodermal pockets. The entrance to the pocket narrows or closes up, and the space surrounding the imaginal bud is the *peripodial cavity*, whose wall is known as the *peripodial membrane*: the latter is continuous with the general hypodermis (Fig. 33). As the imaginal buds develop the peripodial cavities enlarge accordingly and the peripodial membrane becomes attenuated. The mouths of the cavities eventually open and the buds commence to protrude: with the assumption of the prepupal instar the latter are completely everted and appear outside the body. A more detailed account with respect to the development of the wing buds is given on p. 38.

The imaginal buds are exhibited in a relatively simple condition in the larva of *Anopheles*. Those of the head appendages appear at the bases of the existing larval organs which they are destined to replace, and the imaginal head is formed within that of the larva. The largest buds are those of the antennæ, and, of the buds of the mouth-parts, the most conspicuous are those of the future labrum, maxillary palpi and labium. In the thorax two pairs of imaginal buds are present on each segment—a dorsal pair and a ventral pair. The dorsal imaginal buds give rise to the pupal respiratory horns, the wings and the halteres in their respective segments. Each pair of ventral buds forms the legs of its segment. In the abdomen there is a conspicuous pair of dorsal buds at the anal extremity which forms the pupal caudal lamellæ.

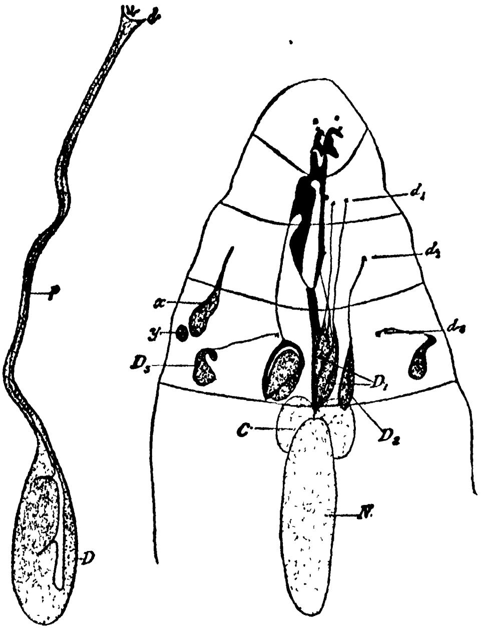

FIG. 209.—IMAGINAL BUDS OF THE LARVA OF *CHORTOPHILA BRASSICÆ* SHOWING THE FILAMENTOUS PEDICELS CONNECTING THEM WITH THE HYPODERMIS.

D_1–D_3, leg buds; d_1–d_3, cutaneous sensory organs (vestiges of larval legs); *x*, wing bud; *y*, bud of haltere; *C*, brain; *N*, ventral nerve centre. × 36. On the left,—imaginal bud D of the fore-leg with its pedicel *p*. × 75. *After* Keilin, 1915.

The researches of Weismann (1864–66), Kowalevsky (1887), van Rees (1888), Pratt (1900), Vaney (1902) and others have shown that the imaginal buds attain increasing complexity in the passage from the lower to the higher members of the Diptera. In the Cyclorrhapha they are deeply sunk into the body, and it is often difficult to trace their connections with the hypodermis owing to the peripodial membrane being reduced in each case to a greatly attenuated cord (Fig. 209). In *Melophagus* the buds, although superficial in position, become disconnected from the hypodermis (Fig. 210).

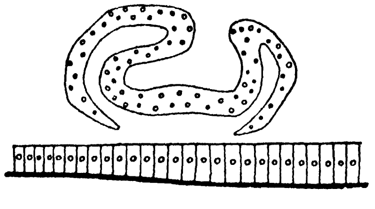

FIG. 210.—THORACIC BUD OF *MELOPHAGUS*.

After Pratt, *Proc. Boston Soc. Nat. Hist.*, 1900.

The most complex feature is exhibited in the imaginal buds of the head: the development of the latter is associated with the position of the cerebral ganglion in the larva, and the fact that the larval head is no longer able to accommodate the developing head of the imago. In *Chironomus* Miall and Hammond (1892) have shown that the cerebral ganglion lies in the larval prothorax, and the imaginal head is formed in relation with the former centre. In a larva about half an inch long, the hypodermis becomes infolded along two nearly longitudinal lines, corresponding to the margins of the larval clypeus. The imaginal buds of the compound eyes and antennæ arise from the inner extremities of these cephalic folds and are thus far removed from the surface. The folds gradually extend backwards into the prothorax until the imaginal buds referred to become closely related to the cerebral ganglion. The posterior prolongation of the folds is accompanied by the formation of a transverse fold which runs back from the junction of the larval head and prothorax (Figs. 211 and 212). During the change to the pupa the parts of the head, thus formed in the larva, assume their final exterior position by a process of eversion, with the result that the now evaginated folds form the wall of the imaginal head and carry the eyes and antennæ with them.

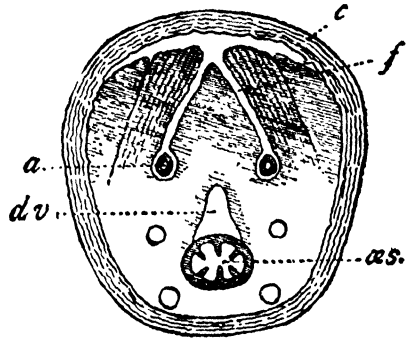

Fig. 211.—Transverse Section through the Junction of the Head and Prothorax of a *Chironomus* Larva showing Invaginations for Imaginal Head.

c, larval cuticle; *f*, longitudinal fold; *a*, antenna of imago; *dv*, dorsal vessel; *œs*, œsophagus. *After* Miall and Hammond.

In *Calliphora*, according to Weismann and Van Rees (Fig. 213), the head becomes invaginated during the later embryonic period into the region which follows it, and its outwardly visible portion is reduced in the larva to a small apical papilla. The invaginated part of the head forms the so-called larval "pharynx" and the true mouth opens into the posterior end of this pouch. A pair of cephalic buds extend as diverticula from the so-called pharynx to the cerebral ganglion (which is located in the metathorax), and the imaginal eyes and antennæ develop from the inner wall of each sac. During the pupal stage the cerebral ganglion and cephalic

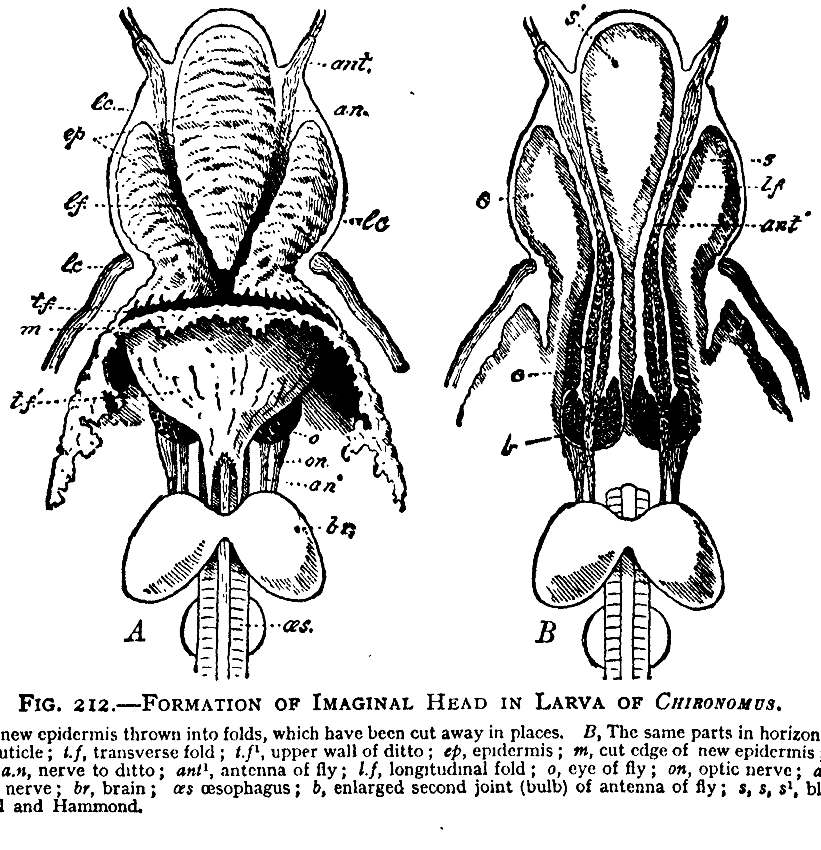

Fig. 212.—Formation of Imaginal Head in Larva of *Chironomus*.

A, The new epidermis thrown into folds, which have been cut away in places. *B*, The same parts in horizontal section; *lc*, larval cuticle; *t.f*, transverse fold; *t.f*^{1}, upper wall of ditto; *ep*, epidermis; *m*, cut edge of new epidermis; *ant*, larval antenna; *a.n*, nerve to ditto; *ant*^{1}, antenna of fly; *l.f*, longitudinal fold; *o*, eye of fly; *on*, optic nerve; *a.n*^{1}, root of antennary nerve; *br*, brain; *œs* œsophagus; *b*, enlarged second joint (bulb) of antenna of fly; *s*, *s*, *s*^{1}, blood-spaces. *After* Miall and Hammond.

buds move forwards until the former come to lie in the prothorax. At the same time the openings of the buds into the "pharynx" widen, and ultimately both the pharynx and its diverticula become confluent, forming a single sac or *cephalic vesicle* (Fig. 213 C). The latter is finally everted through the mouth of the pharynx, and becomes turned inside out to form the completed imaginal head very much as in Chironomus (Fig. 213 D). In the embryo of *Melophagus* Pratt states that the cephalic buds, which ultimately form the adult head, develop as paired dorsal and unpaired ventral thickenings which later on become invaginated. The dorsal pair corresponds to the cephalic buds of *Calliphora*: they are destined to form the dorsa and lateral portion of the imaginal head together with the compound eyes. The ventral cephalic bud has no counterpart in *Calliphora*: it forms the floor of the imaginal head together with the proboscis. Involution of the embryonic head takes place as in *Calliphora* and the cephalic buds become drawn into the secondary "pharynx" thus developed (Fig. 214 A and B). Owing to the early fusion of the dorsal buds the cavities of the latter open into the pharynx by a common connection, but they retain their paired formation posteriorly (Fig. 214 C and D). Finally the dorsal and ventral diverticula combine to form the cephalic vesicle, which subsequently becomes evaginated.

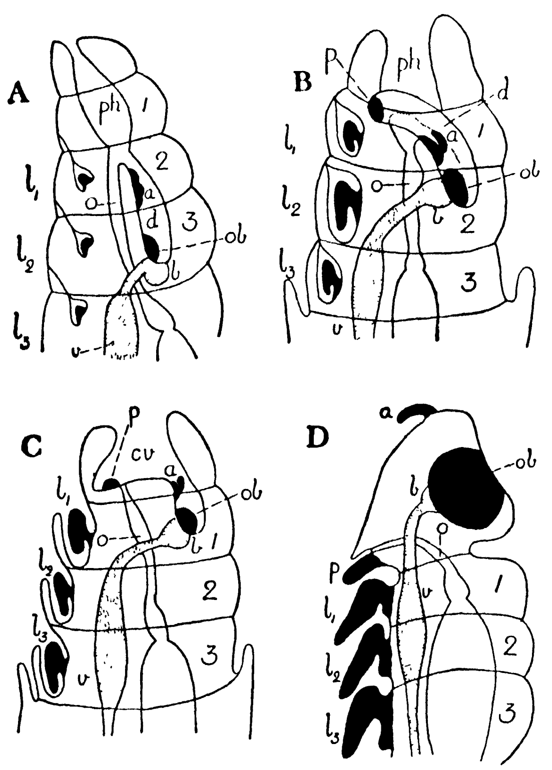

FIG. 213.—DEVELOPMENT OF IMAGINAL BUDS IN THE *MUSCIDÆ*.

A, larva; B—D, pupa; 1-3, thoracic segments; l_1-l_3, leg buds; *ph*, "pharynx"; *o*, œsophagus; *b*, brain; *cv*, cephalic vesicle; *v*, ventral nerve centre; *d*, diverticulum of pharynx; *m*, mouth; *a*, antennal bud; *ob*, optic bud; *p*, proboscis rudiment. Based on Korschelt and Heider *after* Kowalevsky and Van Rees.

The hypodermis of the adult thorax is formed by cell-proliferation of the peripodial membrane of the imaginal buds of that region. The new tissue gradually extends over an increasing area, replacing the larval hypodermis which undergoes disintegration. Areas of new hypodermis, originating from different imaginal buds, become confluent, and an entirely new cell-layer is thus built up. The hypodermis of the adult abdomen is similarly formed from four imaginal buds in each of the first eight segments. These buds differ from those previously described in that they arise as simple thickenings of the larval hypodermis, without any folding taking place. The genitalia arise from pairs of typical imaginal buds in the ventral wall of the two penultimate abdominal segments.

The essential features of the development of the external form of the body in other orders proceeds very much after the manner described in Diptera. The imaginal buds, however, are not deeply insunk as in the Muscidæ, and the complex process which gives rise to the cephalic vesicle does not take place. Furthermore, the buds which form the pupal respiratory horns and caudal lamellæ in *Anopheles* are unrepresented.

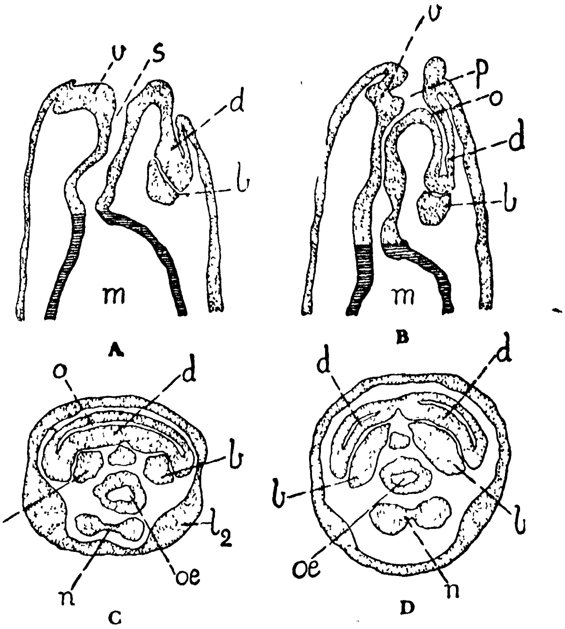

FIG. 214.—DEVELOPMENT OF THE CEPHALIC BUDS IN *MELOPHAGUS* (ECTODERMAL PARTS DOTTED, ENDODERMAL PARTS LINED).

A, longitudinal section of an embryo when the dorsal buds become invaginated. B, later stage when the buds are drawn into the pharynx. C, transverse section of an embryo at stage B. D, do., taken further posteriorly. *b*, brain; *d*, dorsal cephalic bud; l_2, bud of 2nd leg; *m*, mesenteron; *n*, nerve cord; *o*, median opening of dorsal buds; *œ*, œsophagus; *p*, pharynx; *s*, stomodæum; *v*, ventral cephalic bud. Adapted from Pratt, 1900.

2. Development of the Internal Organs.—The great differences in the manner of life of the larva and the imago render many of the larval organs unadapted to perform their functions in the perfect insect, and the necessity for reconstruction consequently arises. The changes involved take place during the late larval and pupal stadia and, although an insect at this period is outwardly quiescent, it is in reality often the seat of intense physiological activity. The extent of the inner transformations varies, not only in different groups of holometabolous insects, but also with regard to individual organs and tissues. Certain parts, including the dorsal vessel and central nervous system, may be relatively little affected, and pursue an uninterrupted course of differentiation. On the other hand, the hypodermis, digestive system, muscles, and salivary glands are profoundly changed. Those larval organs which submit to the greatest alteration undergo dissolution and complete destruction, this breaking down of the tissues being known as *histolysis*. The latter process is generally preceded, and afterwards accompanied, by the generation of new tissues which is termed *histogenesis*. The essential feature of histogenesis is the multiplication of localized groups of cells which withstand the histolytic changes. These cells are the imaginal buds of the internal organs: unlike those of the appendages they do not develop as hypodermal folds. It is by means of their extension and differentiation that the parts concerned are rebuilt to serve the needs of the imago. Various theories have been advanced to account for the physiological processes by which histolysis is accomplished. Kowalevsky (1887), relying upon the researches of Metschnikoff, on the function of leucocytes in the destruction of the tail muscles of Amphibia, demonstrated that in the Muscidæ the blood corpuscles (phagocytes) are the active agents that break down and digest the larval organs. Kowalevsky's conclusions were largely confirmed by Van Rees (1888), and a number of subsequent workers, including Pérez, Mercier, Poyarkoff, and others, have described phagocytosis in different insects. In blood drawn from a pupal insect, such as *Calliphora*, there are found large numbers of "granular spheres" (Körnchenkugeln), 20–35μ in diameter. These bodies are phagocytes distended with inclusions of the tissues which they have attacked (Fig. 215). The expression "Körnchenkugeln" is prevalent in most works dealing with the internal metamorphoses of insects, but was originally applied only to leucocytes distended with muscle debris. Their presence affords the strongest evidence that phagocytosis is taking place. Other authorities, including Anglas (1900) and Berlese (1900–01), see in the phagocytes a different rôle. According to Anglas their function is the secretion of enzymes which bring about tissue-dissolution by a kind of extra-cellular digestion which he terms *lyocytosis*. Berlese has studied histolysis of the muscles in a number of insects and finds that the phagocytes are very active in engulfing fragments of tissue, but, on the other hand, they manifest no digestive capacity, but merely act as transporters of such material to parts of the body where it is required. Bataillon (1893) maintains that histolysis is the result of asphyxiation which is brought about by the lowering of the respiratory activity and the accumulation of CO_2: according to him organs which are no longer functional degenerate as the result.

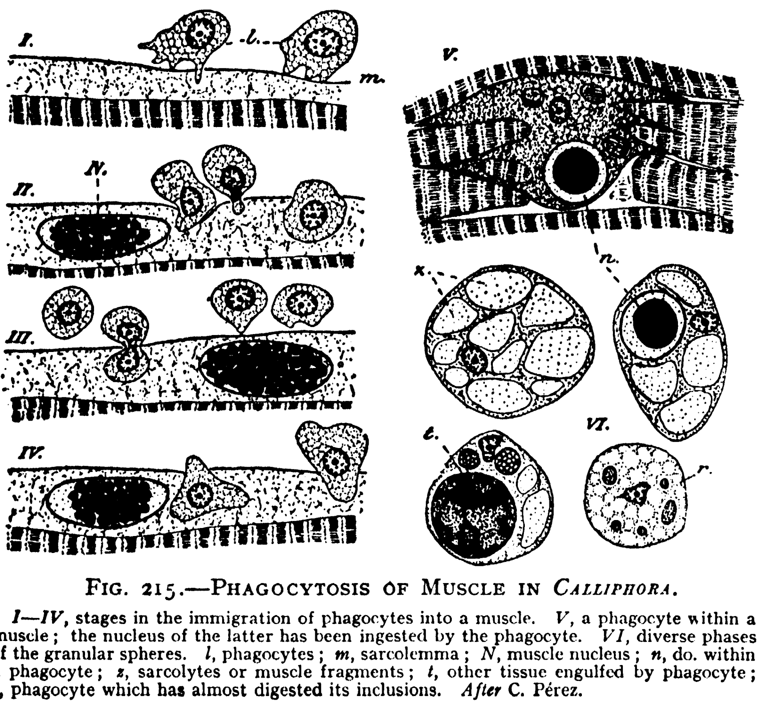

FIG. 215.—PHAGOCYTOSIS OF MUSCLE IN *CALLIPHORA*.

I—IV, stages in the immigration of phagocytes into a muscle. *V*, a phagocyte within a muscle; the nucleus of the latter has been ingested by the phagocyte. *VI*, diverse phases of the granular spheres. *l*, phagocytes; *m*, sarcolemma; *N*, muscle nucleus; *n*, do. within a phagocyte; *s*, sarcolytes or muscle fragments; *t*, other tissue engulfed by phagocyte; *r*, phagocyte which has almost digested its inclusions. *After* C. Pérez.

A number of histologists, including Karawaiew, Terre, Kellogg, Vaney, and Henneguy, in addition to those already mentioned, uphold the theory of degeneration. They claim that too exclusive a rôle has been ascribed to the phagocytes, and that larval organs undergo preliminary chemical dissolution before becoming the prey of those cells. In some cases this process is the only one concerned, in others the phagocytes subsequently intervene. In the Nematoceran *Holorusia*, for example, Kellogg (1901) was unable to detect any evidence of phagocytosis, and believed that tissue dissolution takes place without its agency. In the specialized larva of *Blepharocera*, also one of the Nematocera, where the changes involved are more profound, phagocytosis was predominant. Vaney (1902) similarly found no phagocytosis in *Simulium* and *Chironomus*. Other observers have been unable to find evidence of it in Lepidoptera and Coleoptera. In such cases lyocytosis, or some analogous process, is believed to intervene.

The extensive researches of Pérez on ants (1902) and *Calliphora* (1910) leave little doubt as to the importance of phagocytosis in those insects, and that it attains its maximum activity in the Muscidæ. He finds no evidence of preliminary tissue degeneration and holds that phagocytosis is an all-important process where extensive histolysis is concerned In cases where it is wanting the changes are mainly of an histogenic nature. Pérez's conclusions find support in the work of Poyarkoff (1910) on metamorphosis in the beetle *Galerucella*. Unlike most other workers, he was able to show that phagocytosis in Coleoptera plays an extremely active part in the destruction of organs which undergo marked transformation.

In brief, it may be said that phagocytosis is well established where the changes are great and histolysis intense. It does not, however, appear to be an invariable attribute of metamorphosis and, in certain cases, tissue-dissolution by lyocytosis or other process presumably obtains. Unfortunately knowledge of the inner metamorphoses is less complete in more generalized holometabolous orders, where apparently phagocytosis is less frequent, than in the Diptera.

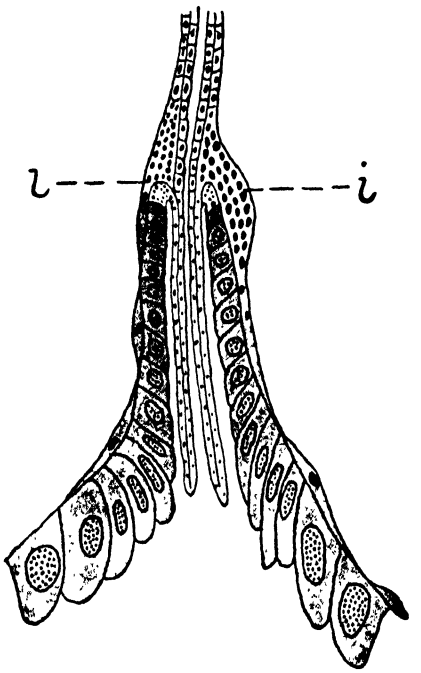

FIG. 216.—MEDIAN LONGITUDINAL SECTION AT THE JUNCTION OF FORE- AND MID-INTESTINE OF *FORMICA RUFA*.

i, annular imaginal bud of fore-intestine. *After* C. Pérez.

The changes undergone by various organs and tissues during histolysis and histogenesis may now be alluded to. Generalizations are often particularly difficult to arrive at for the reason that different investigators are frequently in complete disagreement in their interpretations of the same phenomena. The principal facts, with special reference to Diptera, may be summarized as follows.

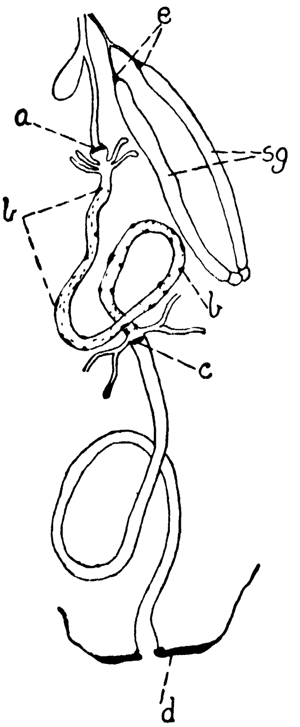

FIG. 217.—ALIMENTARY CANAL AND SALIVARY GLANDS (*sg*) OF A MUSCID LARVA SHOWING IMAGINAL BUDS.

a, of fore-intestine; *b*, of mid-intestine; *c*, of hind-intestine; *d*, of rectum; *e*, of salivary glands. *After* Kowalevsky.

DIGESTIVE SYSTEM. (Figs. 216 and 217.) In most insects phagocytosis plays an unimportant part in the metamorphosis of the alimentary canal. Since the old lining epithelium is sloughed off into the lumen of the gut, and does not undergo dissolution in the hæmocœle, phagocytic intervention is evidently less necessary. The fore-intestine is regenerated by the proliferation of a group of cells forming an annular imaginal bud in the cardiac valve, at the junction of the original ectoderm and endoderm. The transformation of the hind intestine is undergone in a very similar manner from an annular regenerative centre near the insertions of the Malpighian tubes: there are also other imaginal buds associated with the rectum. The mid-intestine is rebuilt by the proliferation of islets of cells situated between the bases of existing epithelial cells. In each part of the gut the original larval epithelium is sloughed off during the process of its replacement,

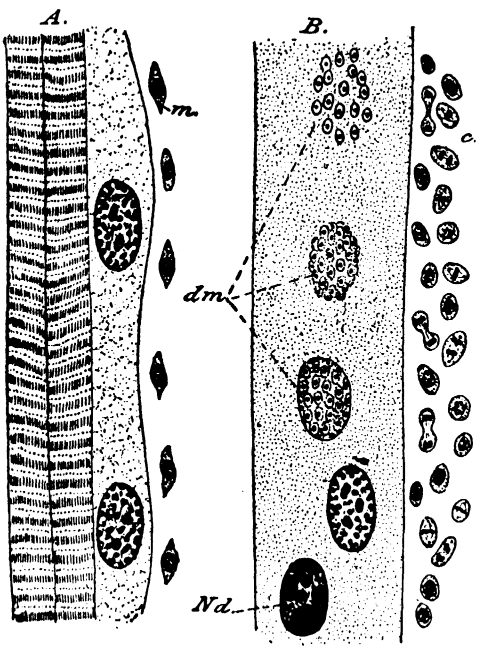

FIG. 218.—METAMORPHOSIS OF A MUSCLE OF *CALLIPHORA* (SEMI-DIAGRAMMATIC).

A, larval stage; *m*, myoblast. *B*, commencement of metamorphosis; *c*, mitosis of myoblasts; *dm*, multiple division of larval nuclei; *Nd*, degenerating nucleus. *After* C. Pérez.

The MALPIGHIAN TUBES in the Muscidæ pass without actual atrophy into those of the imago, but their cells lose differentiation, becoming subsequently reformed. In Hymenoptera the original tubes are destroyed and replaced by new formations. In *Galerucella* there are small replacement cells, very much as in the mid-gut, which give rise to the lining epithelium of the imaginal organs, while the remains of the larval cells are removed by phagocytosis.

SOMATIC MUSCLES. The fate of the muscles varies, not only in different insects, but also with regard to different muscles in the same insect. In *Calliphora* all the more specialized of the larval muscles are destroyed by phagocytes. On the other hand, the more specialized of the imaginal muscles, including those of the legs and genitalia and the transverse sub-hypodermal muscles of the abdomen, are new formations derived from the mesenchyme of imaginal buds. Between these two extremes are numerous transitions: certain of the abdominal muscles pass into those of the imago with but little alteration: other muscles are rebuilt by the agency of myoblasts to a variable degree. The wing-muscles, for example, are formed by myoblasts to such an extent, around three pairs of larval mesothoracic muscles, as almost to amount to new growths. The importance of the rôle of myoblasts in muscle-building varies proportionately as the imaginal muscle departs functionally from the larval muscle from which it is derived. During these changes, the portion of a larval muscle which persists becomes a homogeneous mass and the myoblasts, which are derived from the imaginal buds of the hypodermis, congregate around and penetrate it, thereby building up the composite imaginal muscle (Figs. 218, 219).

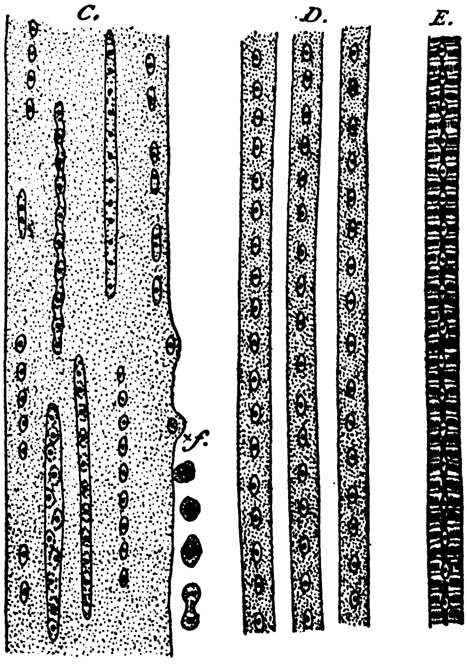

FIG. 219.—METAMORPHOSIS OF A MUSCLE OF *CALLIPHORA* (LATER STAGES).

C, direct division, in chains, of imaginal nuclei; *f*, fusion of myoblasts with differentiated muscle. *D*, cleavage into separate fibres. *E*, final stage of imaginal muscle fibre. *After* C. Pérez.

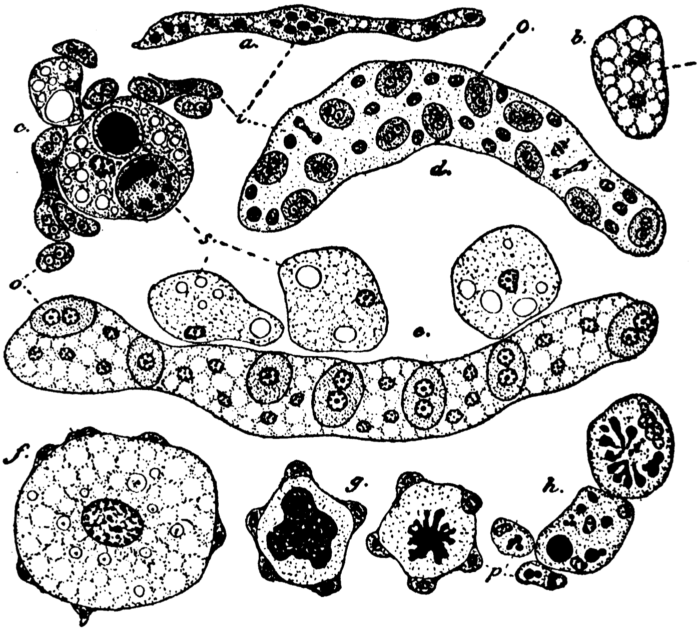

FIG. 220.—ORIGIN OF IMAGINAL FAT-BODY.

a, *b*, in the head and thorax ; *c–e*, in the abdomen in close relation with the imaginal œnocytes ; *s*, granular spheres ; *o*, œnocytes ; *i*, initial cells of imaginal fat-body ; *f–h*, destruction of remaining larval fat-body in the imago by phagocytes *p*. *After* C. Pérez.

According to Berlese the leucocytes engulf fragments of muscle fibres or *sarcolytes* forming the " granular spheres." This material is transported to parts of the body which it serves to nourish. There are also other muscle-fragments containing nuclei which he terms *caryolytes*. The latter are not engulfed by leucocytes, and Berlese traces from them the origin of the imaginal muscles and fat-body. The whole process of the phagocytosis has been reinvestigated with great thoroughness by Pérez, who has shown that Berlese's sarcolytes and caryolytes are simply muscle fragments (in the one case without nuclei and the other with) which are undergoing phagocytosis.

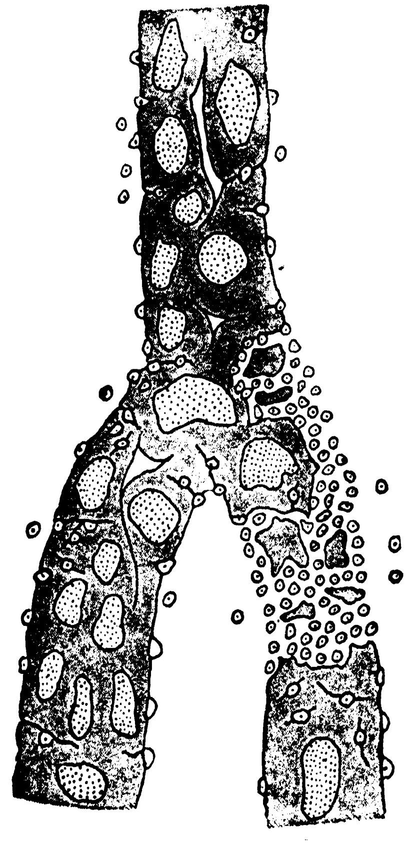

FIG. 221.—HISTOLYSIS OF LARVAL SILK GLAND OF *FORMICA RUFA*. *After* C. Pérez.

FAT-BODY. (Fig. 220.) According to Berlese the larval fat-cells function as *trophocytes*, which play an important part in the accumulation and transformation of albuminoid reserve material, which is utilized in tissue-building during histogenesis. New fat cells, according to him, are derived from caryolytes as already mentioned. In *Calliphora* Pérez finds that certain of the trophocytes are destroyed by phagocytes during the pupal stadium while others persist until after eclosion of the imago, when they are ultimately eliminated in a similar manner. In ants the destruction of the fat-body is much more extensive in the male than in the female. Among most insects the larval fat-body becomes transformed into that of the imago, its albuminoid reserves being then converted into fat. In *Calliphora*, Pérez finds that the imaginal fat-body is a new formation derived from embryonic or mesenchymatous cells situated just beneath the hypodermis.

SALIVARY GLANDS AND SILK GLANDS. These glands degenerate and are usually destroyed by phagocytosis (Fig. 221). The maginal glands are built up by a pair of annular buds situated at the junction of each gland with its duct (Fig. 217). In *Galerucella* Poyarkoff states that the new glands are formed as invaginations at the bases of the maxillæ.

TRACHEAL SYSTEM. The tracheæ undergo a varying amount of reformation in different insects. In *Calliphora* many of the larval tracheæ disappear, their matrix layer being destroyed by phagocytes. The formation of the imaginal tracheæ is due in great part to the proliferation of regenerative centres distributed along the course of the main trunks.

HYPODERMIS. The formation of the hypodermis has already been alluded to, and the final destruction of the larval layer is accomplished by phagocytosis.

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Part III

THE ORDERS OF INSECTS

THE CLASSIFICATION OF INSECTS

THE classification of insects has passed through many changes and most of the systems proposed have been founded upon characters afforded by the mouth-parts, wings and metamorphoses. With the growth of detailed knowledge an increasing number of orders has come to be recognized, some of the most recent writers admitting more than five times as many orders as were known to Linnæus. It will serve no useful purpose to detail the various systems of classification that have been advanced, since almost every authority has adopted a scheme different from those of his predecessors. Handlirsch (1908) has provided an admirable historical résumé of the subject and consequently only those classifications, which are the direct forerunners of the systems current to-day, need be enumerated.

The foundation of the modern classification of insects dates from Brauer (1885) who based his system upon: (1) The presence or absence of wings. (2) The mouth-parts and their changes in ontogeny. (3) Metamorphosis. (4) The number of Malpighian tubes. (5) The nature of the wings, the thoracic segments and certain other features. He recognised the fundamental division of the Insecta into the two sub-classes Apterygogenea and Pterygogenea—members of the former being primitively apterous and those of the latter winged or, in some cases, secondarily apterous. Brauer also did much towards dividing the old assemblage Neuroptera into separate sections each of ordinal value. His classification is as follows:

I. Apterygogenea

1. *Synaptera* (= Collembola + Thysanura).

II. Pterygogenea.

2. *Dermaptera*	HOMOMORPHA
3. *Ephemeridæ* (= Ephemeroptera)	
4. *Odonata*	
5. *Plecoptera*	
6. *Orthoptera genuina* (= Orthoptera + Embioptera)	
7. *Corrodentia* (= Isoptera + Psocoptera + Mallophaga)	
8. *Thysanoptera*	
9. *Rhynchota* (= Hemiptera)	
10. *Neuroptera*	HETEROMORPHA
11. *Panorpatæ* (= Mecoptera)	
12. *Trichoptera*	
13. *Lepidoptera*	
14. *Diptera*	
15. *Siphonaptera* (= Aphaniptera)	
16. *Coleoptera*	
17. *Hymenoptera*	

In 1899 Sharp established a system, partly modelled upon that of Brauer, and introduced the terms Exopterygota and Endopterygota in order to discriminate between those orders in which the wings develop outside the body, and those in which they remain internal until pupation. He further introduced the term Anapterygota to include those apterous orders which have presumably become secondarily wingless. This step, however, has the disadvantage of bringing together distantly related groups. In 1904 Shipley adopted Sharp's classification almost in its entirety, but proposed certain new ordinal names with the double object of doing away with the use of family designations for ordinal purposes, and for the purpose of introducing a system in which the suffix "ptera" is extended to all orders. The classifications of Sharp and Shipley may, therefore, be tabulated together.

Sharp		Shipley
	I. Apterygota.	
1. *Collembola.*		1. *Aptera* (= Thysanura).
2. *Thysanura.*		2. *Apontoptera* (= Collembola
	II. Anapterygota.	
3. *Mallophaga.*		3. *Lipoptera* (= Mallophaga).
4. *Anoplura* (= Siphunculata).		4. *Ellipoptera* (=Siphunculata).
5. *Siphonaptera* (= Aphaniptera).		5. *Aphaniptera.*
	III. Exopterygota.	
6. *Orthoptera* (= Orthoptera + Dermaptera).		6. *Orthoptera.*
7. *Perlidæ* (= Plecoptera).		7. *Plecoptera.*
8. *Psocidæ* (= Psocoptera).		8. *Psocoptera.*
9. *Termitidæ* (= Isoptera).		9. *Isoptera.*
10. *Embiidæ* (= Embioptera).		10. *Embioptera.*
11. *Ephemeridæ* (= Ephemeroptera).		11. *Ephemeroptera.*
12. *Odonata.*		12. *Paraneuroptera* (= Odonata).
13. *Thysanoptera.*		13. *Thysanoptera.*
14. *Hemiptera.*		14. *Hemiptera.*
	IV. Endopterygota.	
15. *Neuroptera* (= Neuroptera + Mecoptera).		15. *Neuroptera.*
		16. *Mecaptera.*
16. *Trichoptera.*		17. *Trichoptera.*
17. *Lepidoptera.*		18. *Lepidoptera.*
18. *Coleoptera.*		19. *Coleoptera.*
19. *Strepsiptera.*		20. *Strepsiptera.*
20. *Diptera.*		21. *Diptera.*
21. *Hymenoptera.*		22. *Hymenoptera.*

In 1904 Börner proposed a system which recognized the same orders as Shipley (although not necessarily under the same names) with the exception that he adopted a threefold division of the Apterygota and revived the ordinal name Corrodentia for the Psocoptera and Mallophaga. Börner's classification may be summarized as follows.

I. APTERYGOTA.

1. *Thysanura* (= Ectognatha). 2. *Diplura* (= Entognatha). 3. *Collembola.*

II. PTERYGOTA.

A. HEMIMETABOLA.

4. *Odonata.* 5. *Agnatha* (= Ephemeroptera). 6. *Dermaptera.* 7. *Plecoptera.* 8. *Isoptera.* 9. *Orthoptera.* 10. *Corrodentia* (= Psocoptera + Mallophaga). 11. *Thysanoptera.* 12. *Rhynchota* (= Hemiptera). 13. *Siphunculata.*

B. HOLOMETABOLA.

14. *Mecaptera.* 15. *Diptera.* 16. *Suctoria* (= Aphaniptera). 17. *Hymenoptera.* 18. *Neuroptera.* 19. *Trichoptera.* 20. *Lepidoptera.* 21. *Coleoptera.* 22. *Strepsiptera.*

In 1908 Handlirsch published a revolutionary system which no longer retained the Insecta as a primary division of the Arthropoda, and involved their dissolution into four classes comprising no less than 34 separate orders. The main features of his system, which is based upon recent and fossil forms, are as given below.

Class I. **Pterygogenea** (= Insecta — Apterygota).

Sub-class I. ORTHOPTEROIDEA.
1. *Orthoptera* (= Saltatoria). 2. *Phasmoidea* (= Phasmidæ). 3. *Diploglossata* (= Hemimeridæ). 4. *Dermaptera.* 5. *Thysanoptera.*

Sub-class II. BLATTÆFORMIA.
6. *Mantoidea* (= Mantidæ). 7. *Blattoidea* (= Blattidæ). 8. *Isoptera.* 9. *Corrodentia* (= Psocoptera). 10. *Mallophaga.* 11. *Siphunculata.*

Sub-class III. HYMENOPTEROIDEA.
12. *Hymenoptera.*

Sub-class IV. COLEOPTEROIDEA.
13. *Coleoptera.* 14. *Strepsiptera.*

Sub-class V. EMBIDARIA.
15. *Embioidea* (= Embioptera).

Sub-class VI. LIBELLULOIDEA.
16. *Odonata.*

Sub-class VII. EPHEMEROIDEA.
17. *Plectoptera* (= Ephemeroptera).

Sub-class VIII. PERLOIDEA.
18. *Perlaria* (= Plecoptera).

Sub-class IX. NEUROPTEROIDEA.
19. *Megaloptera* (= Sialoidea). 20. *Raphidioidea.* 21. *Neuroptera* (= Planipennia).

Sub-class X. PANORPOIDEA.
22. *Panorpatæ* (= Mecoptera). 23. *Phryganoidea* (= Trichoptera). 24. *Lepidoptera.* 25. *Diptera.* 26. *Suctoria* (= Aphaniptera).

Sub-class XI. HEMIPTEROIDEA.
27. *Hemiptera* (= Heteroptera). 28. *Homoptera.*

Class II. **Collembola.**
29. *Arthropleona.* 30. *Symphypleona.*

Class III. **Campodeoidea.**
31. *Dicellura* (Japygidæ). 32. *Rhabdura* (= Projapygidæ + Campodeidæ).

Class IV. **Thysanura.**
33. *Machiloidea* (= Machilidæ). 34. *Lepismatoidea* (= Lepismidæ).

The classification of Handlirsch has not found wide acceptance. It is, however, partly adopted by Brues and Melander (1932) who add to it the more recently discovered orders Zoraptera and Protura and, at the same time, elevate the family Grylloblattidæ to ordinal rank. They recognize altogether 34 orders.

CLASSIFICATION ADOPTED IN THE PRESENT TEXT-BOOK.

Sub-class I. APTERYGOTA

Apterous insects, the wingless condition being primitive, with slight or no metamorphosis. One or more pairs of abdominal appendages present other than genitalia and cerci.

Order 1. THYSANURA.
,, 2. PROTURA.
,, 3. COLLEMBOLA.

Sub-class II. PTERYGOTA

Winged insects which are sometimes secondarily apterous. Metamorphosis very varied, rarely slight or wanting. No abdominal appendages present other than genitalia and cerci.

Division I. EXOPTERYGOTA (=Heterometabola)

Insects passing through a simple and sometimes slight metamorphosis, very rarely accompanied by a pupal instar. The wings develop externally and the larvæ are generalized nymphs.

Order 4. ORTHOPTERA.
,, 5. DERMAPTERA.
,, 6. PLECOPTERA.
,, 7. ISOPTERA.
,, 8. EMBIOPTERA.
,, 9. PSOCOPTERA.
,, 10. ANOPLURA.
,, 11. EPHEMEROPTERA.
,, 12. ODONATA.
,, 13. THYSANOPTERA.
,, 14. HEMIPTERA.

Division II. ENDOPTERYGOTA (=Holometabola)

Insects passing through a complex metamorphosis always accompanied by a pupal instar. The wings develop internally and the larvæ are usually specialized.

Order 15. NEUROPTERA.
,, 16. MECOPTERA.
,, 17. TRICHOPTERA.
,, 18. LEPIDOPTERA.
,, 19. COLEOPTERA.
,, 20. STREPSIPTERA.
,, 21. HYMENOPTERA.
,, 22. DIPTERA.
,, 23. APHANIPTERA.

The ordinal name Anoplura is here given to include the Mallophaga and Siphunculata which are now generally admitted to be closely related. The inclusion of the Anoplura and Aphaniptera among the Pterygota is based upon the probability that their apterous condition is secondary, and has been acquired for so extended a period that all traces of alary rudiments have been eliminated from their ontogeny. It is noteworthy, moreover, that the absence of wings is by no means an unknown phenomenon in those orders to which the Anoplura and Aphaniptera are most nearly related.

The Exopterygota are connected with the Endopterygota by the hemipterous families Aleyrodidæ and Coccidæ, both of which exhibit clear indications of a pupal stage: an incipient pupa can also be recognized among the Thysanoptera.

Literature on Classification

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SUB-CLASS APTERYGOTA

THE Apterygota are universally distributed but, owing to their small size and concealed habits, probably the majority of the world's species have so far escaped discovery. About 1,200 species are known : without exception they are wingless insects and there is every reason to believe that this apterous condition is of a primitive and not a secondary origin. As a rule they retain the superlinguæ in a more generalized condition than other insects, and the presence of abdominal appendages is a very characteristic feature. Metamorphosis is always of a very slight and gradual nature or is more often absent. It is principally by a comparative study of the members of this sub-class that it is possible to trace the origin, evolution, and affinities of the Insecta as a whole. For a bibliography and general discussion of the Apterygota, reference should be made to a paper by Crampton (1916).

Order I. THYSANURA (Bristle-tails)

MOUTH-PARTS ECTOGNATHOUS OR ENTOGNATHOUS, ADAPTED FOR BITING. ANTENNÆ MANY-JOINTED. COMPOUND EYES PRESENT OR ABSENT. ABDOMEN II-SEGMENTED, WITH A VARIABLE NUMBER OF STYLIFORM LATERAL APPENDAGES, AND BEARING AT ITS APEX EITHER (1) A PAIR OF MANY-JOINTED CERCI WITH OR WITHOUT A MEDIAN CERCIFORM PROCESS ; OR (2), MORE RARELY, A PAIR OF UNJOINTED FORCEPS. TRACHEAL SYSTEM PRESENT : MALPIGHIAN TUBES PRESENT OR ABSENT. METAMORPHOSIS SLIGHT OR WANTING.

This order includes the most primitive of all insects and is very widely distributed ; about a dozen species have been found in the British Isles. Its members are ancient survivals of a formerly more extensive group and persist to-day largely owing to a concealed life in the soil, in rotting wood, under stones, or in the leaf-deposits of forest floors ; a considerable number also live in the nests of ants and termites. Unlike many Collembola they are not usually found among living herbage. The " silver fish," *Lepisma saccharina* (Fig. 222), occurs in buildings in Europe and North America, where it is destructive to paper, book-bindings, etc., and *Thermobia domestica* Pack. frequents the warmth afforded by bakehouses and kitchens. *Petrobius maritimus* (Fig. 223) inhabits rocky places on the British coasts, close to the edge of the sea. Although the order includes a number of minute forms, the majority of species attain a larger size than is found in the Collembola, and *Heterojapyx soulei*, for example, measures about 50 mm. long. Most species are brownish, grey, or white in colour, and the scaled forms exhibit a metallic sheen.

External Anatomy.—In the Machilidæ and many Lepismidæ the body is clothed with scales, but in the remaining families these structures are usually wanting. The antennæ are long and filiform, often consisting of 30 or more joints. Compound eyes are well developed in the Machilidæ, where they are approximated or contiguous dorsally: in the Lepismidæ they are considerably reduced, and among the Entotrophi they are wanting. Ocelli are generally absent, but in the Machilidæ median and paired organs of this nature are evident: they are curiously variable in form, and are regarded by Grassi as being intermediate in structure between simple and compound eyes. The head often exhibits the epicranial suture and in *Campodea* (Fig. 224) there is also a transverse occipital suture; both the labrum and clypeus are well developed. The mouth-parts are normal and exserted in the Ectognatha: in the Entognatha they are sunk within the head as in the Protura and Collembola. In *Petrobius*, which is selected as an example of the Ectognatha, the mouth-parts are of the most primitive type found among insects (Fig. 9). The mandibles are elongated, 2-jointed, pointed organs, and are each provided with a well-defined projecting molar area. In their general features they closely resemble those of certain of the higher Crustacea. The superlinguæ are exceptionally

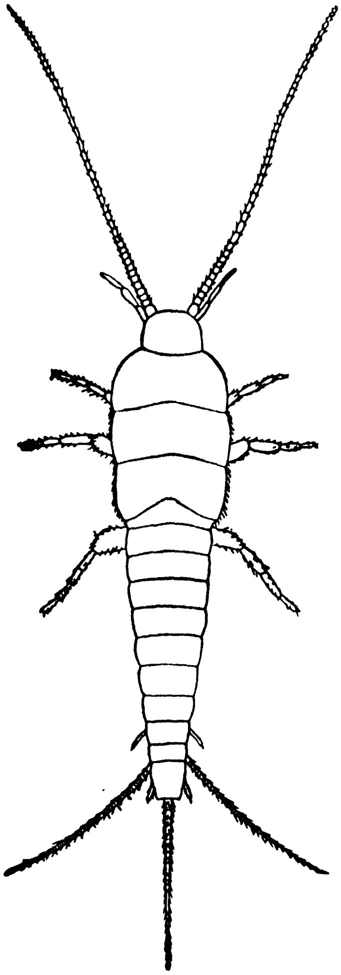

Fig. 222.—*Lepisma saccharina* (Magnified) Britain.
After Lubbock.

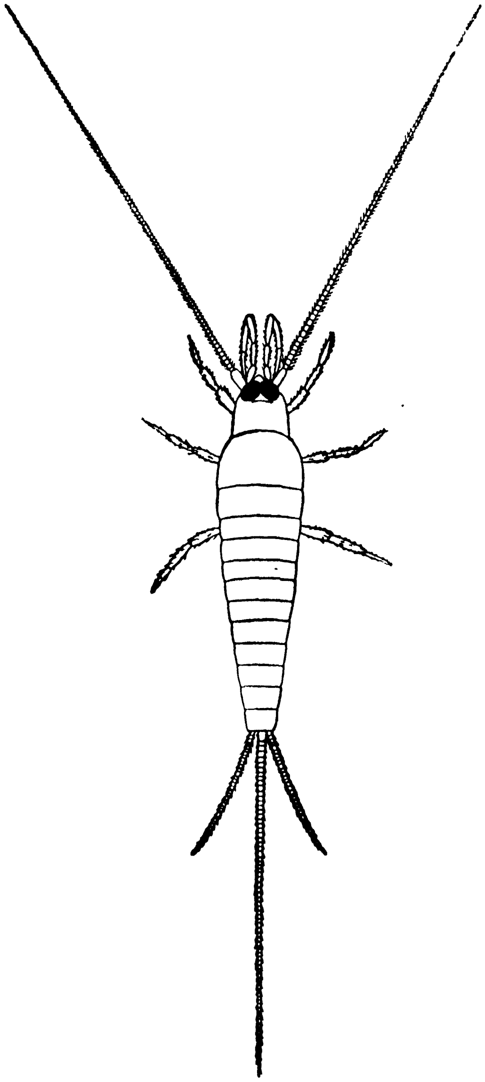

Fig. 223.—*Petrobius* (*Machilis*) *maritimus* (magnified). Britain.
After Lubbock.

well developed: each organ is attached by membrane to the base of the hypopharynx, and exhibits differentiation into two lobes together with a vestigeal palp-like appendage. The maxillæ are composed of the typical sclerites and their palpi are 7-jointed. In the labium the mentum and submentum are broad plates, the prementum is paired, and the palpi are 3-jointed. Paired glossæ and paraglossæ are present and both of these structures are longitudinally subdivided into two lobes. In *Lepisma* the mandibles are each composed of a single sclerite, and in the labium the glossæ and paraglossæ are single organs on either side. In the Entognatha the mouth-parts are less primitive to the extent that they resemble those of the Collembola more closely than the same organs in the Ectognatha. The mandibles are unjointed and toothed at their apices: in *Campodea*, and *Anajapyx* each bears, near its extremity, a small plate-like appendage or "lacinia mobilis." The superlinguæ in all cases are simple undivided plates. The maxillary lobes are paired, but the maxillary palpi are very short in *Japyx*, and vestigial in *Campodea*. The labium is much reduced: the ligula usually consists of a pair of small glossæ and broader bristle-bearing lobes, or paraglossæ. In some cases, as in *Japyx sylvestris* Carp. the ligula consists of a single pair of lobes. In the latter genus the labial palpi are small, 1-jointed structures; in *Campodea* and *Anajapyx* they are vestigeal and in *Parajapyx* they are totally atrophied.

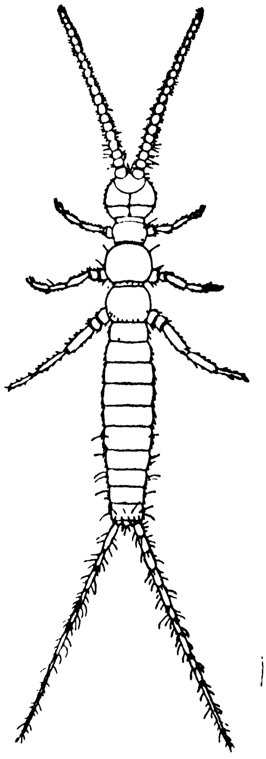

FIG. 224.—*CAMPODEA* (× *circa* 15). BRITAIN.
After Lubbock.

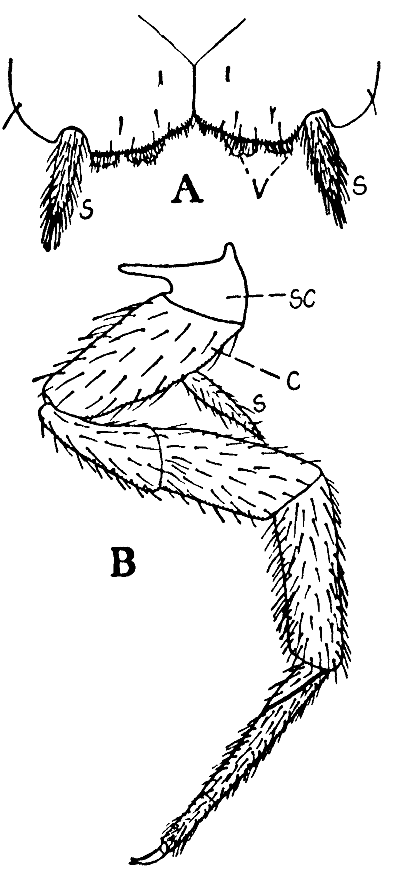

FIG. 225.—*PETROBIUS MARITIMUS*. BRITAIN.

A, hind margin of 5th abdominal segment showing vesicles *v* and styli *s*. B, left leg of 3rd pair; *c*, coxa; *s*, stylus; *sc*, subcoxa.

The legs exhibit variation in the number of tarsal joints; they are usually 3-jointed in the Machilidæ, 3 or 4-jointed in the Lepismidæ and single-jointed in the Entognatha. In all cases the tarsal claws are paired. In the Machilidæ (Fig. 225) the coxæ of the 2nd and 3rd pairs of legs bear a small pair of movable unjointed styli.

The abdomen is composed of 11 segments: in the Ectognatha the 11th tergum is prolonged into a median cerciform appendage, and in the Entognatha its counterpart is seen in the small suranal plate. The abdominal sterna (Fig. 225) carry a variable number of pairs of styli similar to those found on the two hind pairs of coxæ in the Machilidæ. In the latter family a pair is present in relation with each sternum from 2–9 inclusive: in the Projapygidæ and Japygidæ on 1–7, in *Campodea* on 2–7 and in the Lepismidæ on 7–9 or 8–9. In *Campodea* there is also a pair of larger appendages in relation with the 1st sternum. In addition to styli most Thysanura carry segmentally arranged protrusible vesicles (Fig. 225) : the latter are placed in close association with the styli but are situated rather nearer the mid-ventral line of the body. These vesicles are capable of being extended by means of blood-pressure, and can be withdrawn into their segment by the aid of special muscles. Their function is obscure but they may, as Oudemans and Haase have suggested, serve a respiratory purpose. In *Machilis* and *Petrobius* there are two pairs of vesicles in relation with each sternum from the 2nd to the 5th and a single pair on the 1st, 6th, and 7th sterna. In *Præmachilis* there is a single pair in relation with sterna 1 to 7 ; in *Campodea* and *Anajapyx* in relation with 2 to 7 ; in *Japyx* they are confined to the 2nd sternum and in *Projapyx* and *Lepisma* they are wanting.

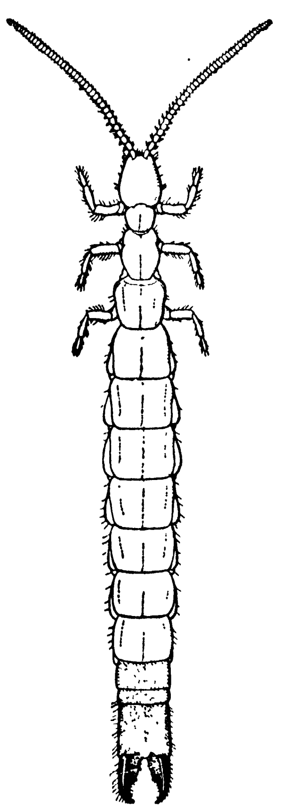
FIG. 226.—*HETEROJAPX* SP. AUSTRALIA. (× 3.)

The *genitalia* attain their fullest development in the Ectognatha and consist of one or two pairs of gonapophyses. In the male there is a definite ædeagus of simple form and the gonapophyses are usually imperfectly jointed. In *Petrobius* there is a single pair of these appendages which is borne on the 9th sternum : in *Machilis* and *Præmachilis* paired gonapophyses are present in relation with the 8th and 9th sterna respectively. In the female the ovipositor is usually well developed, often long, and consists of two pairs of many-jointed appendages carried on the same sterna as the corresponding organs of the male. Among the Entognatha the genitalia are rudimentary or wanting in both sexes.

The abdomen is usually terminated by a pair of slender cerci which may consist of 50 or more joints: on the other hand, in the Projapygidæ (Fig. 229) they are short and stout with less than a dozen joints. In the Japygidæ, cerci are replaced by unjointed forceps (Fig. 226). In the Ectognatha there is, in addition, a median jointed, cerciform process which often exceeds the whole body in length : morphologically this structure is to be regarded as a prolongation of the 11th tergum and is, therefore, not a true appendage.

Internal Anatomy.—The *alimentary canal* (Fig. 227) is a simple straight tube, except in *Lepisma* where the hind intestine presents a single convolution. The proportions of the three divisions of the gut vary greatly in different genera. Thus in *Anajapyx* the œsophagus is of great length, and extends into the 4th segment of the abdomen, while the stomach is greatly reduced. There is a large gizzard in *Lepisma* and in this genus, and in *Machilis*, enteric cœca are present. Salivary glands appear to be universally present, but the Malpighian tubes are inconstant. In the Ectognatha the latter organs are well developed and number 12 to 20 in the Machilidæ, and 4 to 8 in the Lepismidæ. In *Campodea* and *Anajapyx* the Malpighian tubes are represented by papillæ—about 16 in the former case and 6 in the latter: in *Japyx* these organs are totally wanting. The *nervous system* (vide Hilton, *Ann. Ent. Soc. Am.* 1917) is exhibited in its most generalized condition in the Machilidæ where there are 3 thoracic and 8 abdominal ganglia, and the longitudinal connectives retain their double nature throughout the length of the ventral nerve cord (Fig. 65 A). There are similarly 8 abdominal ganglia in the Lepismidæ and *Japyx*, while in *Campodea* and *Anajapyx* the 7th and 8th ganglia are united into a common centre. The *tracheal system* exhibits important differences in the several families. In the Machilidæ there are 9 pairs of spiracles: the 1st pair is located between the pro- and mesothorax, the 2nd pair is placed near the hinder border of the mesothorax, and the remaining pairs are placed on the 2nd to 8th abdominal segments. The tracheæ associated with each spiracle remain unconnected with those of adjacent segments. In the Lepismidæ there are 10 pairs of spiracles which belong to the 2nd and 3rd thoracic and the first 8 abdominal segments. In this family the tracheal system is relatively highly developed; there is a common longitudinal tracheal trunk passing down either side of the body, and there is a transverse trunk in each segment uniting the tracheæ of opposite sides. *Campodea* (Fig. 125) exhibits a very inferior development of the tracheal system: there are 3 pairs of spiracles which are thoracic in position, and the tracheæ associated with each spiracle remain isolated and distinct. In *Japyx solifugus* (Fig. 113) there are 11 pairs of spiracles of which 4 are thoracic, and 7 are abdominal. The 1st, 2nd and 4th pairs correspond with the 3 pairs of thoracic spiracles in *Campodea*: the 3rd pair is situated on the metathorax in advance of the 4th pair. A longitudinal trachea unites the tracheæ on either side of the body into a single system, but there is only a single delicate transverse commissure which is situated near the junction of the 9th and 10th abdominal segments. In *J. isabellæ* there are 9 pairs of spiracles; those homologous with the 2nd and 4th pairs in *J. solifugus* being unrepresented. In *Projapyx* there are 10 pairs—3 thoracic and 7 abdominal: in *Anajapyx* there are 9 pairs of which the 1st and 2nd correspond with the 1st and 3rd in *Japyx solifugus*.

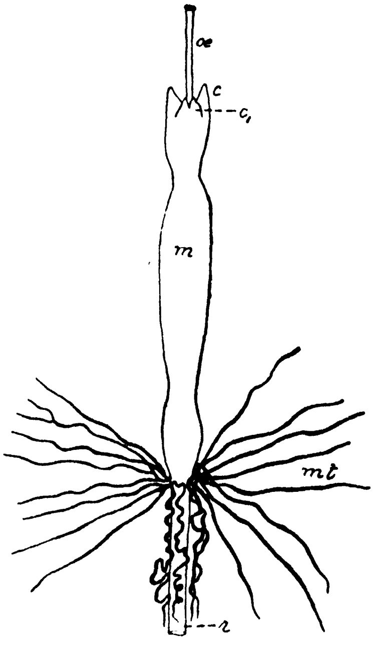

FIG. 227.—ALIMENTARY CANAL OF *PETROBIUS*.

œ, œsophagus; *c*, large cœca; c_1, smaller do.; *m*, mid-intestine; *mt*, Malpighian tubes *r*, rectum.

After Oudemans.

The *dorsal vessel* is notable on account of the forward extension of the heart into the mesothorax: in *Japyx* the heart is composed of ten chambers. According to Grassi, alary muscles are wanting but delicate structures of this nature are described by Oudemans in *Petrobius*. A pair of *posterior glands*, possibly of a repugnatorial nature, opens at the apices of the cerci in the Projapygidæ and are homologous with similar glands in the Symphyla and Diplopoda.

The *reproductive organs* (Fig. 228) exhibit important morphological differences in the five families. As regards the female organs, there is a single pair of polytrophic ovarioles in *Campodea* while in other members of the order they are panoistic. In *Japyx* there are seven metamerically arranged ovarioles on either side : in *Petrobius* there is a similar number of ovarioles but their segmental disposition is no longer evident : in *Lepisma* there are five ovarioles to a side and there is likewise no segmental arrangement: in *Anajapyx* the segmental arrangement is maintained but the number of ovarioles to a side is reduced to two. In all cases the vagina is practically non-existent, and the two oviducts only combine just before opening by means of a common genital aperture on the 8th sternum. The male organs in *Campodea* consist of a single large testis, and a very short vas deferens on either side. In *Anajapyx* each testis consists of two lobes which closely resemble the two ovarioles of the ovary: in *Lepisma* there are three double lobes, segmentally arranged, to each testis, and in *Petrobius* there are three single lobes which discharge close together near the apex of the vas deferens. In the latter genus each vas deferens is double throughout the greater part of its course, the two canals thus formed being united by a series of five transverse connecting tubes. In both *Japyx* and *Lepisma* the vasa deferentia are convoluted and of considerable length. A ductus ejaculatorius, when present, is always short and opens on the ædeagus.

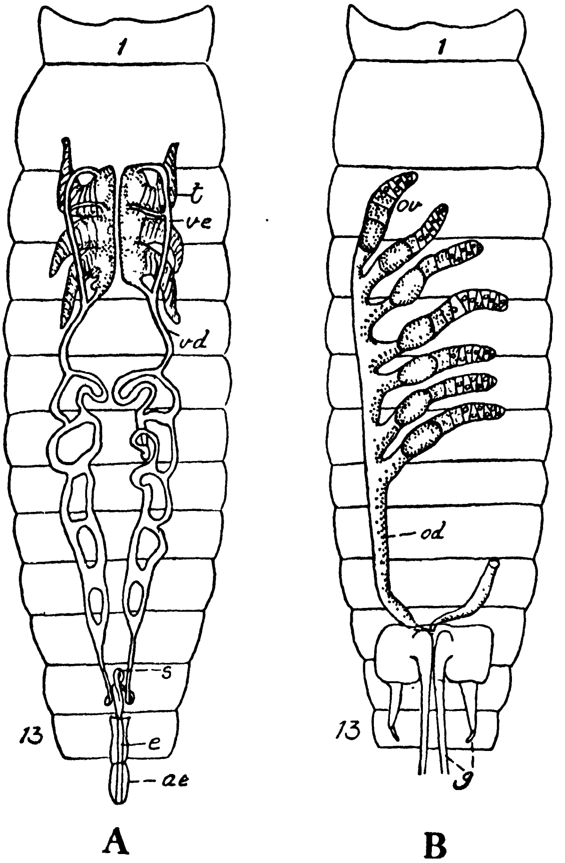

FIG. 228.—REPRODUCTIVE ORGANS OF *PETROBIUS*. VENTRAL SIDE.

A, male; B, female. 1, 1st thoracic segment; 13, 10th abdominal do.; *t*, testis; *ve*, vas efferens; *vd*, vas deferens; *e*, ejaculatory duct; *s*, blind sac; *ae*, ædeagus; *ov*, ovariole; *od*, oviduct; *g*, genitalia. Adapted from Oudemans.

Post-Embryonic Growth. — Post-embryonic development has been principally observed in the Machilidæ and has been studied by Heymons (*Sitz. Ges. naturf. Freunde, Berlin* 1906, p. 253) and by Verhoeff (*Zool. Anz.* 38, p. 524). There appear to be at least six instars, including the adult, and in the first two the young insects are devoid of scales, the genitalia are as yet undeveloped, and there are no styli on the thoracic coxæ. In the third instar scales are evident and small coxal styli are present. In the fourth instar the gonapophyses are apparent, though short, and in the female their jointed character does not develop until later. Other changes are evident in the mouth-parts, and the completed details of their structure are not assumed until after the final ecdysis. The changes undergone are less profound than those of the Orthoptera, but their simplicity is largely correlated with the absence of wings. In the Japygidæ, Silvestri states that the eggs and young forms are protected beneath the body of the female. The growth changes are slight, there being no increase in the number of antennal segments and most difference is seen in the forceps. The latter are toothless and straight in the first instar and assume the adult condition in the next instar.

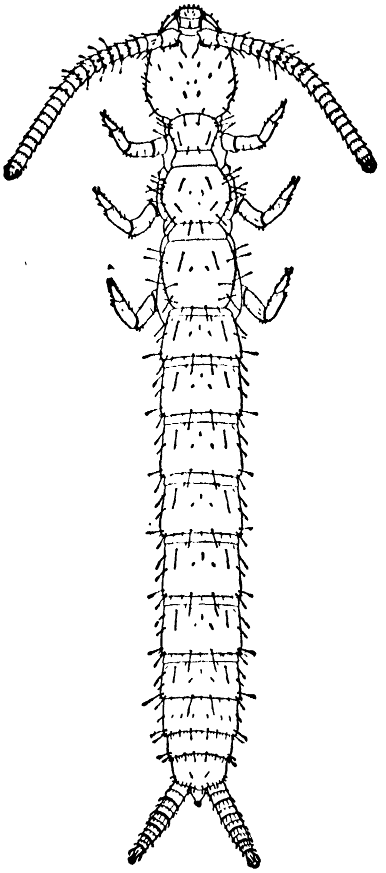

FIG. 229.—*ANAJAPYX VESICULOSUS* (magnified) ITALY.

After Silvestri, 1905.

Literature.—Most of what is known concerning the structure of the Thysanura is to be found in the writings of a few authors. The most comprehensive work is that of Grassi (1887). For the Machilidæ vide Oudemans (1888); for the Lepismidæ, Escherich (1905); for the Projapygidæ, Silvestri (1905), and the Japygidæ, Verhoeff (1904).

Classification.—The order is divisible into two sub-orders and five families as follows:

Sub-order I. ECTOGNATHA

Mouth-parts exserted, normal. Abdomen terminated by a median caudal filament and paired cerci. Malpighian tubes well developed.

FAM. 1. MACHILIDÆ.—COMPOUND EYES LARGE, OCELLI PRESENT. ABDOMINAL SEGMENTS 1–7 WITH EXSERTILE VESICLES: STYLI USUALLY PRESENT ON THORACIC COXÆ AND ON ABDOMINAL SEGMENTS 2–9. *Petrobius, Machilis, Præmachilis,* etc.

FAM. 2. LEPISMIDÆ.—COMPOUND EYES SMALL, OCELLI ABSENT. ABDOMEN USUALLY WITH EXSERTILE VESICLES: STYLI ABSENT FROM THORACIC COXÆ AND USUALLY PRESENT ON ABDOMINAL SEGMENTS 7–9, OR 8–9. *Lepisma, Acrotelsa, Nicoletia,* etc.

Sub-order II. ENTOGNATHA

Mouth-parts sunk within the head. Abdomen terminated by paired cerci or forceps, median filament wanting. Malpighian tubes greatly reduced or absent.

FAM. 3. CAMPODEIDÆ.—FIRST ABDOMINAL SEGMENT WITHOUT STYLI: ABDOMEN TERMINATED BY CERCI WHICH ARE IMPERFORATE APICALLY. *Campodea, Lepidocampa,* etc.

FAM. 4. PROJAPYGIDÆ.—STYLI PRESENT ON FIRST ABDOMINAL SEGMENT: ABDOMEN TERMINATED BY CERCI WHICH ARE PERFORATE APICALLY. *Projapyx, Anajapyx.*

FAM. 5. JAPYGIDÆ.—STYLI PRESENT ON FIRST ABDOMINAL SEGMENT: ABDOMEN TERMINATED BY FORCEPS. *Japyx, Heterojapyx,* etc.

General Literature on Apterygota and Thysanura

CRAMPTON, 1916.–The Orders and Relationships of Apterygotan Insects. *Journ. N.Y. Ent. Soc.* 24. **ESCHERICH, 1905.**–Das System der Lepismatiden. *Zoologica,* 43. **FERNALD, 1890.**–The Relationships of Arthropods. *Johns Hopkins*

Univ. Studies, 4. **GRASSI, 1887.**–Anat. Comp. dei Tisanuri e Consid. gen. sull organizzazione degli Insetti. *Att. Acad. d. Lincei* (4), 4. **HAASE, 1899.**–Vide p. 50 **HANDSCHIN, 1929.**–Apterygota; in *die Tierwelt Deutschlands.* Teil. 16. Jena **HOULBERT, 1924.**–Thysanoures, etc., de France. I. *Encycl. Scient. Paris* **LUBBOCK, 1873.**–Monograph of the Collembola and Thysanura. London. **OUDEMANS, 1888.**–Beit zur Kenntnis der Thysanura und Collembola. *Bijd. tot Dierk* 16 (Trans. of Dutch paper of 1887.) **SILVESTRI, 1905.**–Nuova Contrib. alla conoscenza dell' *Anajapyx vesiculosus. Ann. Scuola d'Agric., Portici,* 6 (and many other papers in the same journal). **VERHOEFF, 1904.**–*Zur* Vergleich. Morph. und Syst. der Japygiden. *Arch. Naturg.* **1.**

Order 2. PROTURA (Myrientomata)

MINUTE INSECTS WITH ENTOGNATHOUS PIERCING MOUTH-PARTS: ANTENNÆ AND COMPOUND EYES WANTING. ABDOMEN 12-SEGMENTED; FIRST THREE SEGMENTS EACH WITH A PAIR OF SMALL APPENDAGES. TRACHEAL SYSTEM PRESENT OR ABSENT. MALPIGHIAN TUBES REPRESENTED BY PAPILLÆ. METAMORPHOSIS SLIGHT, CHIEFLY EVIDENT AS AN INCREASE IN NUMBER OF THE ABDOMINAL SEGMENTS.

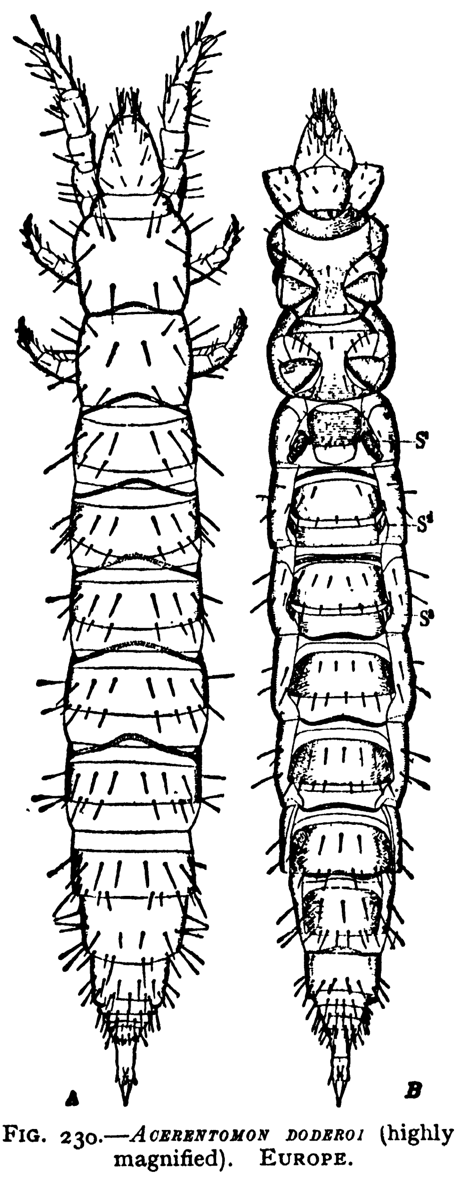

FIG. 230.—*Acerentomon doderoi* (highly magnified). EUROPE.

A, dorsal; *B*, ventral; S, styli. *After* Silvestri, 1907.

The Protura are minute whitish organisms—the largest species scarcely attain 2 mm. in length, and the majority are usually much smaller. They are widely distributed and occur in England and other European countries, in India and in the United States. Owing to their very small size Protura are easily overlooked, but they are not rare in certain types of moist soil, in peat and in turf: they have also been met with under stones and beneath bark. The order was first recognized by Silvestri in 1907, from Italy, and has since been very fully studied by Berlese (1909) whose monograph is accompanied by a wealth of anatomical detail. Owing to the absence of antennæ, the Protura have the habit of walking with the fore-legs held upwards in front of the head, these appendages probably functioning as tactile organs.

External Anatomy (vide Prell 1913).—The head is pyriform, narrowing anteriorly. There are no visual organs but on either side there are a pair of minute structures termed by Berlese *pseudocelli* which are perhaps homologous with the post-antennal organs of Collembola (vide p. 227). The *labrum* is in the form of a pointed projection, while the mandibles and maxillæ are withdrawn into the head (Fig. 231). The former appendages are stylet-like and adapted for piercing. The maxillæ are divided into an outer and an inner lobe, and the palpi are 3- or 4-jointed: either the inner or both lobes are modified into piercing organs. The labium is composed of a basal sclerite and a pair of pointed glossæ, but there appear to be no structures clearly homologous with paraglossæ: the labial palpi are short and 2- or 3-jointed (Fig. 232). No organs comparable with superlinguæ are described by Berlese. The thorax is clearly defined with the first segment considerably reduced: the legs are long with 1-jointed tarsi, each of which is terminated by a single claw. The abdomen is very long and slender: in the newly hatched insect it is 9-segmented and, during post-embryonic development, three more segments are added by intercalary growth between the last two segments. This anamorphosis, or increase in the number of segments after emergence from the egg, is a Diplopod and Chilopod character. The first three abdominal segments each carry a pair of small appendages (Fig. 230): in the Eosentomidæ they are 2-jointed, the second joint being reduced and provided with a protrusible vesicle. In the Acerentomidæ only the first pair is 2-jointed: the others consist of a single minute joint. Cerci are absent in the order, and the name Protura is derived from the simple telson-like 12th segment.

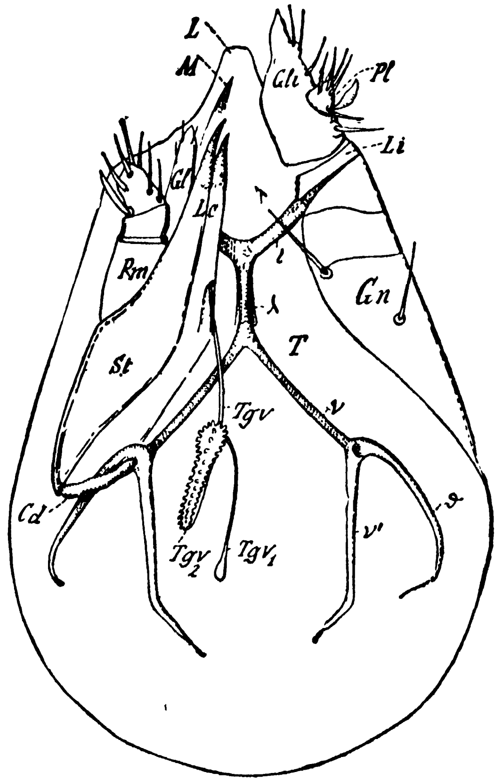

FIG. 231.—*ACERENTULUS TIARNEUS*. VENTRAL VIEW OF HEAD SHOWING RIGHT MAXILLA, LEFT LOBE OF LABIUM (*Gli*) AND TENTORIUM (*T*).

Cd, cardo; *Gl*, galea; *Gn*, gena; *L*, labrum; *Lc*, lacinia; ***Li***, basal sclerite of labium; *M*, apex of mandible; ***Pl***, labial palp; *Pm*, maxillary palp; *st*, stipes; ***Tgv***, tubules of maxillary gland. *After* Berlese. *Redia*, 1909.

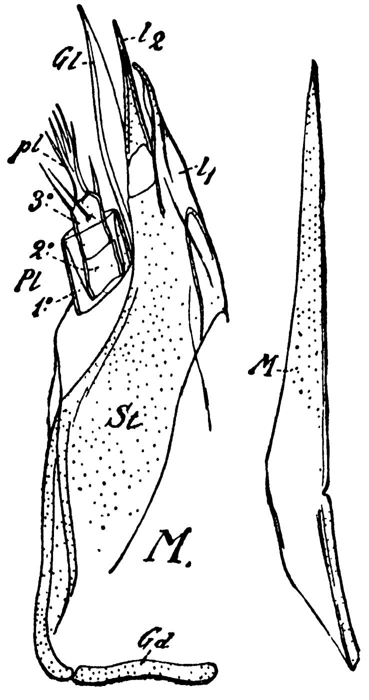

FIG. 232.—*ACERENTULUS CONFINUS*

M, **right** mandible; *M_1*, left maxilla; *Cd*, cardo; *st*, stipes; *Pl*, palp; *Gl*, galea; *$l_1 l_2$*, lacinia. *After* Berlese. *Redia*, 1909.

Internal Anatomy (Fig. 233).—The alimentary canal is a simple straight tube and its most extensive region is the large cylindrical stomach. Two pairs of maxillary glands and a pair of labial (salivary) glands are present. The Malpighian tubes are represented by six uni- or bi-cellular papillæ disposed in two groups of three. The nervous system consists of the brain; with fused infra-œsophageal and prothoracic ganglia, while there are separate ganglia in the remaining thoracic and the first six abdominal segments. The connectives throughout are double. The terminal ganglion is larger than those preceding and there is a supplementary ganglion on each pedal nerve at the bases of the legs. In those forms possessing a *tracheal system* (Fig. 234) the latter communicates with the exterior by means of two pairs of spiracles—one pair on the mesothorax and the other pair on the metathorax. There is no communication between the tracheæ associated with the spiracles of one side or of opposite sides of the body. The *reproductive system* in the female consists of a pair of panoistic ovaries and oviducts; the latter combine to form a short vagina which opens by a median pore between the 11th and 12th abdominal segments. Each ovary extends, when mature, from the metathorax into the 9th abdominal segment and is homologous with a single panoistic ovariole in other insects. The germarium is situated in the reflexed apex of the ovary and from it is derived a single chain of egg-cells. In the male the testes are a pair of elongate sacs which are united anteriorly about the level of the mesothorax. The vasa deferentia are closely coiled tubes which enter the ædeagus separately: the latter organ is protruded between the 11th and 12th segments. The germarium is apical and the remainder of the testes contains spermatozoa in various stages of development. The *circulatory system* is of a peculiar nature: there is no pulsatory dorsal vessel but its position is occupied by a longitudinal trough-like filament termed by Berlese the *pericardial cord*.

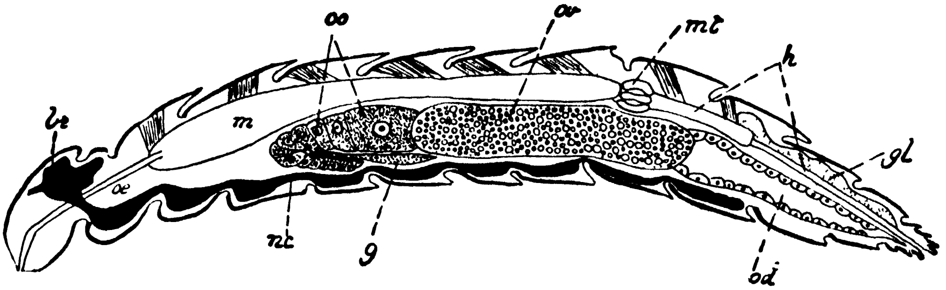

FIG. 233.—*Acerentulus confinus*, Female : General Anatomy.

br, brain; *g*, germarium; *gl*, abdominal gland; *h*, hind intestine; *m*, mid-intestine; *mt*, excretory papillæ; *nc*, nerve cord; *od*, oviduct; *oe*, fore-intestine; *oo*, oocytes; *ov*, mature ovum. Adapted from Berlese. *Redia*, 1909.

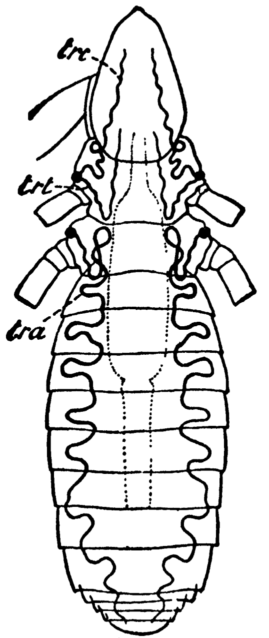

FIG. 234.—Tracheal System of *Eosentomon* (much retracted).

trc, cephalic trachea; *trt*, thoracic do.; *tra*, abdominal do. *After* Berlese *Redia*, 1909.

Affinities.—The systematic position of the Protura cannot be regarded as being settled and is, at present, largely a matter of opinion. Berlese and Comstock maintain that they form a class of their own—the Myrientomata. On the other hand, Silvestri and Börner place them among the Insecta. The mouth-parts are insectan in character and are not unlike those of suctorial forms among Collembola. The differentiated thorax and three pairs of legs are also insectan features, together with the reduction of the abdominal appendages. Those who maintain the view that the Protura represent a class of their own, base their conclusions mainly upon anamorphosis, the absence of antennæ, and the position of the genital aperture. It is noteworthy that the absence of antennæ is probably a secondary feature, and these organs are reduced to the condition of minute papillæ in many insect larvæ. The number of abdominal segments, furthermore, agrees with the primitive number found in embryo insects, and the most important non-insectan character is the occurrence of anamorphosis.

Classification.—The order is divided by Berlese into two families as follows:—

FAM. I. ACERENTOMIDÆ.—SECOND AND THIRD ABDOMINAL APPENDAGES 1-JOINTED. TRACHEAL SYSTEM ABSENT. *Acerentomon, Acerentulus, Protentomon.*

FAM. II. EOSENTOMIDÆ.—SECOND AND THIRD ABDOMINAL APPENDAGES 2-JOINTED. TRACHEÆ PRESENT. *Eosentomon* (including *Protapteron*).

Literature on Protura

BERLESE, 1909.—Monographia dei Myrientomata. *Redia,* 6. **MILLS, 1932.**—Catalogue of the Protura. *Bull. Brooklyn Ent. Soc.* 27. **PRELL, 1913.**—Die Chitinskelett von *Eosentomon. Zoologica,* 64. **SCHEPOTIEFF, 1909.**—Studien über niedere Insecten. *Zool. Jahrb., Abt. Syst.* 28. **SILVESTRI, 1907.**—Descrizione di novo genere di Insetti Apterygoti, rappresentanti di un novo Ordine. *Boll. Lab. Zool. Portici.* 1. **TUXEN, 1931.**—Monographie der Proturen. I. *Zeits. Morph. u. Biol. Tiere.* 22. **WOMERSLEY, 1927–29.**—Notes on the British Protura, etc. *Ent. Month. Mag.* 63–65.

Order 3. COLLEMBOLA (Spring-tails)

MOUTH-PARTS ENTOGNATHOUS, PRINCIPALLY ADAPTED FOR BITING: ANTENNÆ USUALLY 4-JOINTED, COMPOUND EYES ABSENT. ABDOMEN 6-SEGMENTED, USUALLY WITH 3 PAIRS OF APPENDAGES, i.e. AN ADHESIVE VENTRAL TUBE ON SEGMENT I, A MINUTE HAMULA ON III, AND A FORKED SPRINGING ORGAN ON IV. THEY RARELY POSSESS A TRACHEAL SYSTEM AND THERE ARE NO MALPIGHIAN TUBES. METAMORPHOSIS ABSENT.

Collembola are small insects rarely exceeding 5 mm. in length, and occur in almost all situations. They are found in the soil, in decaying vegetable matter, among herbage, under bark of trees, etc. A few species frequent the nests of ants and termites, others occur on the surface of fresh water and several are littoral or marine: *Anurida maritima*, for example, is daily submerged by each tide. The only condition which seems essential for their welfare is a certain amount of moisture, for they are rare in very dry situations. The order is world-wide and is remarkable for the extensive distribution of many of its genera and species. *Isotoma*, for example, is known from both polar regions, and is distributed throughout Europe and many parts of N. America. It has been recorded from Argentina, Sumatra, the Hawaiian Isles, Azores, etc. Among individual species, *Bourletiella hortensis* occurs in Europe, N. America, Tierra de Fuego and Japan, while *Achorutes armatus* has an even wider range.

Collembola vary very much in coloration. Many are of a uniform dull blue-black, as in *Anurida*: others are green or yellowish with irregular patches of a darker colour: a few species are banded, some are all white, one or two are bright red while metallic forms are not infrequent. In habits they are saprophagous or phytophagous.

External Anatomy (Figs. 235–239).—In the greater number of species the body is clothed with hairs but some genera, notably *Tomocerus* and *Lepidocyrtus*, are scaled. The hairs vary in shape, often on different regions of the body: they may be simple and tapering, clavate, flattened and partially resembling scales, or plumose. The antennæ vary greatly in length and the distal joints may be secondarily annulated. They are typically 4-jointed: the maximum number of six joints is found in *Orchesella*. In the Neelidæ the antennæ may be shorter than the head, while in some of the Entomobryidæ they are much longer than the whole body. Sensory organs of varied types are usually present on the last two joints and take the form of cones, rods, pits or papillæ. A variable number of ocelli are generally present on either side of the head behind the antennæ: there are never more than eight to a side and often much fewer. In some Collembola they are absent as in *Onychiurus* (*Lipura*) and *Cyphoderus*. Immediately behind the antennæ there is a very characteristic structure known as the *post-antennal organ*. The latter assumes a great variety of forms among different genera, being simple and ring-like in *Isotoma*, in the form of a rosette in *Anurida*, while in *Onychiurus* it attains considerable complexity of structure. It is evidently a sensory organ from the fact that it has a special nerve-supply, and the thinness of its cuticular investment suggests its capability for receiving external stimuli, possibly of an olfactory nature. The *mouth-parts* (vide Folsom, 1899) are deeply withdrawn into the head and are greatly elongated, which allows of their freedom of movement when they are protruded. Their deeply-seated position is a secondary acquisition and has been brought about in the following manner. In the embryo, the sides of the head develop from a pair of lateral evaginations of the germ band. These evaginations eventually fuse with the developing fundaments of the labrum and labium and, in this way, form a kind of enclosing box which, by further growth, comes to surround the remaining mouth-parts. The mouth-cavity is roofed over by the labrum and clypeus, both these sclerites being exhibited, for example, in *Anurida*. The mandibles (Fig. 236) are slender organs usually with toothed extremities. The maxillæ each consist of a complex apical portion or "head" which possibly represents a lacinia. In some species a digit-like palpifer is present: it carries a vestigial palp and the galea. The cardo and stipes are variable in form and sometimes rod-like. The superlinguæ are well developed lamellate structures overlying the hypopharynx: as a rule they are undivided but in *Isotoma palustris* they are bilobed. The hypopharynx is provided with a pair of elongate pedicels which articulate proximally with the cardines of the maxillæ. The labium is very much reduced and, although it exhibits evidences of a paired structure, neither glossa nor paraglossæ are separately developed. Labial palpi have been detected in the early embryo but as a

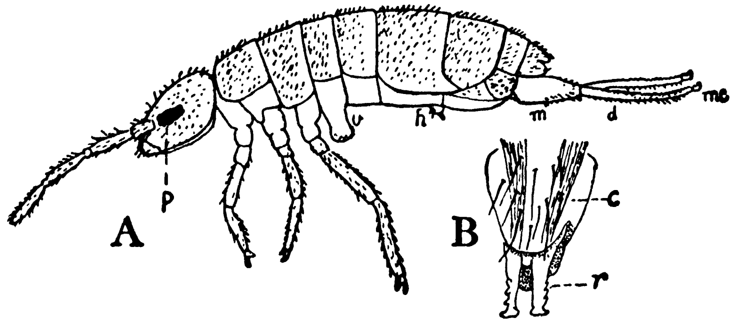

FIG. 235.—STRUCTURAL DETAILS OF COLLEMBOLA.

A, *Axelsonia*. *p*, pigment surrounding eyes; *v*, ventral tube; *h*, hamula; *m*, manubrium; *d*, left dens and mucro *mc*. Adapted from Carpenter. B, *Tomocerus*; *h*, hamula; *c*, corpus; *r*, ramus. *After* Willem, 1900.

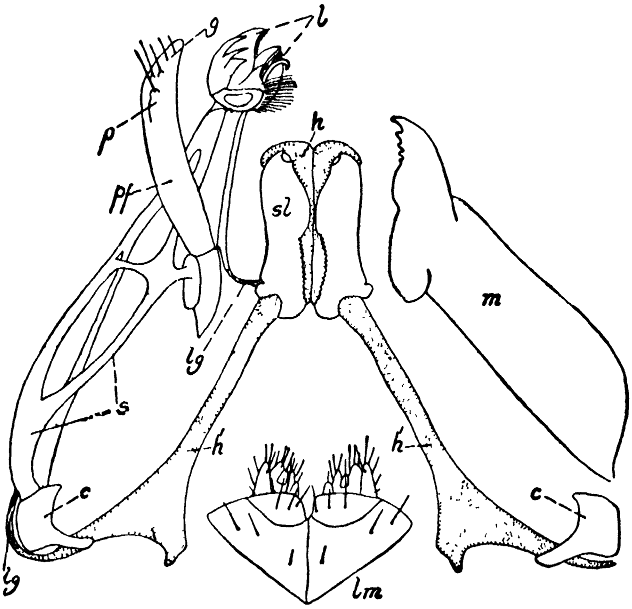

FIG. 236.—MOUTH-PARTS OF *ORCHESELLA*, DORSAL VIEW.

c, cardo; *g*, galea; *h*, hypopharynx and its pedicels h^1; *l*, lacinia; *lg*, ligament; *lm*, labium; *m*, right mandible; *p*, maxillary palp; *pf*, palpifer; *s*, stipes; *sl*, superlingua. Partly *after* Folsom.

rule they subsequently atrophy. In *Neanura* and its allies the mouth-parts are specialized for sucking and piercing: the labrum and labium together form a conical tube enclosing the rest of the mouth-parts, the latter being modified into stylets. The thorax, in the more generalized forms, consists of three very similar segments but in the Entombryidæ the prothorax is greatly reduced, and its tergum is undeveloped. In the Symphypleona the thorax becomes intimately fused with the abdomen and its segmentation is, to a large extent, obsolete. The legs have no true tarsal joints and the tibiæ generally terminate in a pair of claws, an upper and a lower, but the latter may be vestigeal or wanting. The abdomen is composed of six segments only: in this respect Collembola differ from all other insects and, at no stage in development, are there known to be more than that number present. In some of the Arthropleona the 4th and 5th, or 4th to 6th segments undergo fusion, while in the Symphypleona the first four segments are almost entirely undifferentiated. On the ventral aspect of the first segment, in all Collembola, there is a bilobed structure known as the *ventral tube* (vide Hoffmann, *Zool. Anz.* 1904). It is formed by the union of the first pair of embryonic abdominal appendages, and consists of a basal column containing a pair of protrusible vesicles. The latter are commonly in the form of shallow sacs but in some genera they are long and tubular. The cavity of the ventral tube freely communicates with that of the body and contains blood: the vesicles are everted by means of blood pressure, while they are withdrawn by the contraction of special muscles. Many divergent opinions have been expressed with respect to the function of the ventral tube, and the view which has received the widest support is the one which regards it as an adhesive organ, enabling the insect to walk over smooth or steep surfaces. In this connection it is noteworthy that the surface of the vesicles is moistened by the secretion of cephalic glands which is discharged into the commencement of the *ventral groove* (Fig. 237). The latter is a cuticular channel passing down the middle ventral line of the body: it arises from a point just behind the labium and terminates on the anterior aspect of the ventral tube. Many Collembola retain a minute pair of appendages on the 3rd abdominal segment. They are fused proximally to form a basal piece or *corpus*, while their distal portions remain free and are termed the *rami*. The organ thus formed is variously known as the *retinaculum* or *hamula*, and it serves to retain the furcula in position, when the latter is stowed away under the abdomen while not in use The majority of Collembola carry a pair of partially fused appendages in relation with the 4th abdominal segment. They constitute the *furcula*, or springing organ, which enables the insect to take sudden leaps into the air—hence the name of " spring-tails " which is commonly applied to the members of this order. When released from the hamula, the extensor muscles of the furcula contract, and the latter organ is forcibly

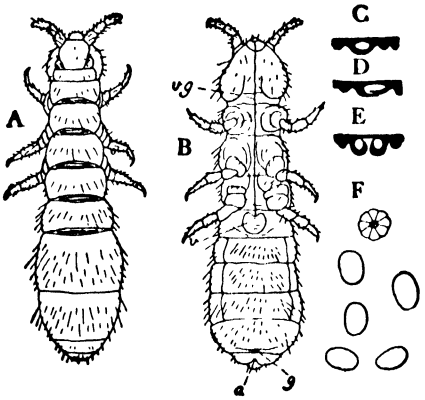

FIG. 237.—*ANURIDA MARITIMA.*

A, dorsal. B, ventral; *a*, anus; *g*, genital pore *v*, ventral tube; *vg*, ventral groove. C, D, E, transverse sections of ventral groove in regions of the head, prothorax and metathorax respectively. F, eyes and post-antennal organ, right side.

pulled downwards and backwards so as to strike the ground and propel the insect a relatively long distance into the air. The common basal piece of the furcula is termed the *manubrium* which carries a pair of distal arms or *dentes*: each dens carries a very variably shaped claw-like process or *mucro*. The furcula varies greatly in development; in *Entomobrya*, for example, it extends, when at rest, to beyond the ventral tube; in *Achorutes* it is often very short, while in *Neanura* and *Anurida* it is wanting. The sexes are similar in Collembola, there being no genitalia: the genital aperture is placed near the hind margin of the 5th sternum, while the anus is located on the 6th sternum.

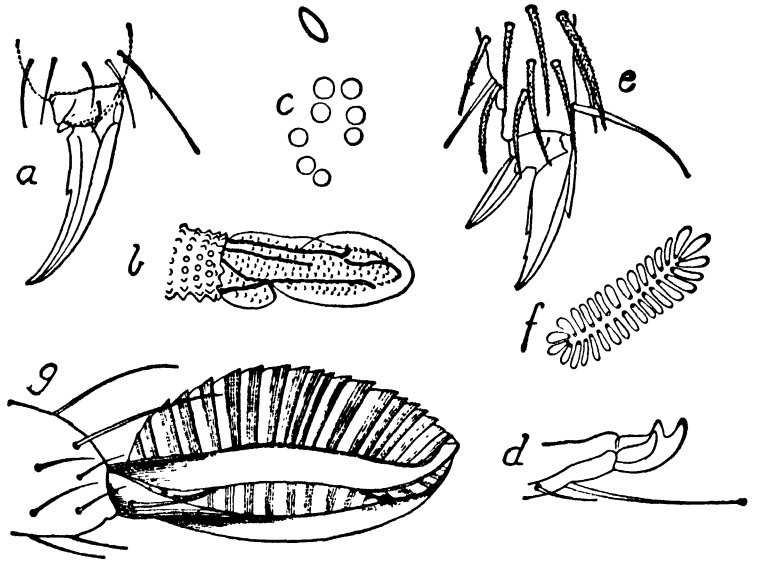

FIG. 238.—STRUCTURAL DETAILS OF COLLEMBOLA.

a, *Podura*, claw of left leg; *b*, left mucro; *c*, *Isotoma*, eyes and postantennal organ; *d*, left mucro; *e*, *Lepidocyrtus*, claws of left leg; *f*, *Onychiurus*, right postantennal organ; *g*, *Sminthurides*, left mucro. Adapted from Folsom.

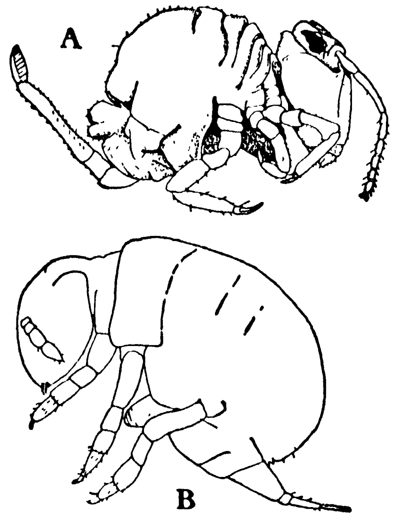

FIG. 239.—COLLEMBOLA, SYMPHYPLEONA (magnified).

A, *Sminthurides aquaticus*. *After* Willem. B, *Neelides folsomi*. *After* Caroli.

Internal Anatomy (Fig. 240).—The *alimentary canal* is a simple straight tube, passing from the mouth to the anus without presenting any convolutions. The greater portion is formed by the extensive mid-intestine and the latter, in *Neelus*, is subdivided into four subequal chambers. With the exception of salivary glands, there are no appendages of the alimentary canal. The central *nervous system* is considerably specialized and consists of the cerebral ganglia and a ventral nerve-cord composed of four ganglionic centres—the sub-œsophageal and three thoracic ganglia, which are united by double connectives. There are no separate abdominal ganglia, the nerve centres of that region having fused with the metathoracic ganglion. In the Sminthuridæ the ventral ganglia are closely merged together, there being no intervening connectives. The *heart*, in the more generalized forms, consists of a series of six chambers with paired lateral ostia and alary muscles at each of the constrictions. Anteriorly, the heart is prolonged into the aorta and in *Anurida* the latter vessel surrounds the fore-intestine in the form of a cylinder which opens in the head beneath the cerebral ganglia. There are no Malpighian tubes and *excretion* is chiefly performed by the fat-body. The latter contains numerous concretions which, according to Willem (1900), are composed of urate of soda. These concretions increase in size with the age of the individual and are not eliminated from the insect. It is noteworthy that an analogous method of excretion is met with in the renal vesicles of Ascidians.

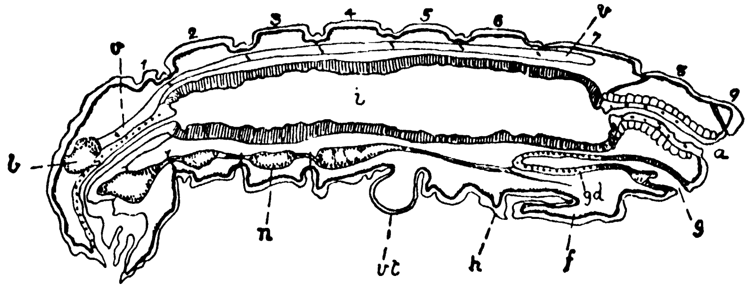

FIG. 240.—*ACHORUTES VIATICUS*, LONGITUDINAL SECTION.

a, anus; *b*, brain; *f*, furcula; *g* genital pore; *gd*, gonoduct; *h*, hamula; *i*, mid-intestine; *n*, nerve cord; *v*, dorsal vessel; *vt*, ventral tube. *After* Willem, 1900.

In addition to the fat-body, the epithelium of the stomach performs an excretory function. Folsom and Welles (*Stud. Univ. Illinois* 2, 1906) have shown that the mid-gut cells contain concretions of a similar nature to those found in the fat-body. These congregate in the inner halves of the cells, which divide off from the remainder, and are periodically discharged into the stomach cavity. They are removed from the body during each ecdysis, and a regeneration of the epithelium takes place.

Respiration in the majority of Collembola is cutaneous but in *Sminthurus*, *Sminthurides* and *Actaletes* tracheæ are present (Fig. 241). They are best developed in the first mentioned genus where there is a single pair of simple spiracular openings between the head and prothorax. Tracheal branches are distributed to the head, legs and abdomen, but no anastomosis takes place between the tracheæ of opposite sides of the body.

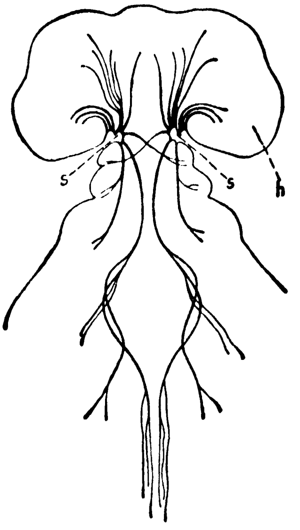

FIG. 241.—*SMINTHURUS FUSCUS*. TRACHEAL SYSTEM.

h, head; *s*, spiracle. *After* Willem, 1900.

The *reproductive system* is of an extremely simple nature: the gonads consist of a pair of large sacs, their ducts are extremely short and they unite to form the vagina or ejaculatory canal as the case may be. The ovaries contain groups of vitellogenous cells and developing eggs but there is no arrangement into ovarioles, and the testes are filled with dense masses of developing spermatozoa. Unlike other insects, the germarium in both the ovaries and testes is lateral and not apical in position. Accessory organs are usually wanting in both sexes.

Post-Embryonic Growth.—The eggs of Collembola are smooth and spherical, usually cream-coloured, and are deposited in small groups. The newly-hatched insects are white excepting for an area of dark pigment surrounding the ocelli. Several ecdyses are passed through before full growth is attained, but the changes involve no important differences between the young and the adult insects. They chiefly consist of an increase in size and in pigmentation, and a further differentiation of the ioints of the antennæ and furcula.

The species *Sminthurus viridis* has been more fully studied than any other. It feeds on the leaves of various plants, especially Leguminosæ and, according to MacLagan (1932), the optimum conditions for growth are a humidity near saturation and soil with a *p*H of about 6·5. Under these conditions, and a temperature of about 13° C., the maximum number of eggs laid per individual is about 120 : they are coated with soil voided through the anus. The incubation period is near 26 days and about 48 days elapse from eclosion to sexual maturity. There are eight instars and the last ecdysis takes place after attaining sexual maturity. As an adult the insect lives for about 15 days: the life span, from the egg onward, is approximately 2½ months and there are five generations in the year.

A very characteristic feature of Collembola is a tendency to gregariousness or the massing together of enormous numbers of individuals comprising both adult and immature forms. This behaviour has been noted in various countries (vide Turk, *Nature*, June, 1932) but its significance is unknown. In some cases it may be connected with an abundance of a particular food or in others with migration.

Literature on Collembola.—Faunistic and taxonomic writings on the order are numerous : these, along with the morphological literature, have been listed up to 1906 (vide Imms). A general monograph on these insects needs to be written as the treatise of Lubbock (1873) is now out of date. Among the more important taxonomic works, useful to students of the British species, those of Schött (1893) and Linnaniemi (1907) may be mentioned, together with the papers by Carpenter and Evans (*Proc. Roy. Phys. Soc. Edinburgh*, 1900) and by Womersley (*Proc. Roy. Irish. Acad.* 39, Section B., 1930). The chief work on the structure of Collembola is that of Willem (1900), while the detailed anatomy of *Anurida* has been investigated by Fernald (1890) and Imms (1906) and that of *Tomocerus* (*Macrotoma*) by Sommer (1885). The classification of the order is due to Börner (1913) and a useful synopsis of the system elaborated by this author is given by Shoebotham (*Ann. Mag. Nat. Hist.* (8), 19, 1917).

Classification.—The following classification is based upon that of Börner except that the older, and well defined, subdivision of the Arthropleona into two families is adopted.

Sub-order I. ARTHROPLEONA

Body more or less cylindrical and elongate: segmentation of abdomen well defined or, rarely, with 5th and 6th or 4th to 6th segments partially fused.

FAM. 1. PODURIDÆ.—PROTHORAX WELL DEVELOPED WITH A DEFINITE TERGUM. CUTICLE USUALLY GRANULATED. *Podura, Achorutes, Anurida, Onychiurus,* etc.

FAM. 2. ENTOMOBRYIDÆ.—PROTHORAX GREATLY REDUCED AND WITHOUT A TERGUM. CUTICLE NOT GRANULATED. *Entomobrya, Tomocerus, Isotoma, Actaletes, Cyphoderus,* etc.

Sub-order II. SYMPHYPLEONA

Abdomen subglobular, segmentation obliterated or vestigial.

FAM. 3. NEELIDÆ.—ANTENNÆ STOUT, NOT LONGER THAN HEAD: THORAX VERY LARGE. *Neelus, Megalothorax, Neelides.*

FAM. 4. SMINTHURIDÆ.—ANTENNÆ MORE SLENDER, LONGER THAN HEAD : THORAX NOT EXCEPTIONALLY LARGE. *Sminthurus, Sminthurides, Bourletiella,* etc.

Literature on Collembola

BECKER, 1910.–Bau des postantennal organs der Collembolen. *Zeits. wiss. Zool.* 94. **BÖRNER, 1913.**–Die Familien der Collembolen. *Zool. Anz.* 41. **DAVIES, 1927.**–On the Tracheal System of Collembola. *Quart. Journ. Mic. Sci.* 71. —— **1928.**–The Effect of Variation in Relative Humidity on Collembola. *Brit. Journ. Exp. Biol.* 6. **DENIS, 1928.**–Etudes sur l'Anatomie de la tête de quelques Collemboles. *Arch. Zool. Exp.* 68. **FOLSOM, 1899.**–The Anatomy and Physiology of the Mouth-parts of *Orchesella cincta*. *Bull. Mus. Comp. Zool. Harvard,* 35. **HANDSCHIN, 1926.**–Collembola: in Schultze, *Biologie der Tiere Deutschlands.* T. 25. —— **1929.**–Vide p. 222. **HOULBERT, 1924.**–Vide p. 222. **ICHIKAWA, 1931.**–On the Renewal of the Mid-Intestinal Epithelium of Collembola. *Mem. Coll. Sci. Kyoto Univ.* B, 7. **IMMS, 1906.**–Anurida. *L'pool. Marine Biol. Mem.* 13. **LINNANIEMI, 1907–12.**–Die Apterygoten-Fauna Finlands. *Acta. Sci. Faun. Fl. Fennica.* 40. **LUBBOCK, 1873.**–Vide p. 222. **MACLAGAN, 1932.**–An Ecological Study of the "Lucerne Flea" (*Smynthurus viridis*). *Bull. Ent. Res.* 23. **PHILIPTSCHENKO, 1907.**- Anatom. Studien über Collembola. *Zeits. wiss. Zool.* 85. **SCHÖTT, 1893.**–Zur Systematik und Verbreitung palæartischer Collembola. *Kongl. Svenska Vet.-Akad. Handl.* 25. **SOMMER, 1885.**–Ueber *Macrotoma plumbea*. *Zeits. wiss. Zool.* 41. **STREBEL, 1927–32.**–Biologische Studien an einheimischen Collembolen. *Zeits. wiss. Insektenbiol.* 23 ; *Zeits. Morph. u. okol.* 25 ; *Zool. Anz.* 84. **WILLEM, 1900.**–Recherches sur les Collemboles et Thysanoures. *Mem. Sav. Etr. Acad. Roy. Belg.* 58.

Vide also :—

BOELITZ, 1933.–Beitrage zur Anatomie und Histologie der Collembolen. *Zool. Jahrb., Abt. Anat.* 57.

SUB-CLASS PTERYGOTA

Order 4. ORTHOPTERA (Cockroaches, Stick Insects, Grasshoppers, etc.)

INSECTS WITH TYPICAL BITING MOUTH-PARTS: SUPERLINGUÆ VESTIGIAL OR ABSENT: LIGULA 4-LOBED. VENATION OF A GENERALIZED TYPE, OFTEN WITH ARCHEDICTYON AND SUPERNUMERARY VEINS. FORE-WINGS ELONGATE AND NARROW, MODIFIED INTO SOMEWHAT HARDENED TEGMINA: HIND-WINGS MEMBRANOUS, AND MORE DELICATE, WITH AN EXTENSIVE ANAL AREA: APTEROUS AND BRACHYPTEROUS FORMS COMMON. ABDOMEN USUALLY WITH JOINTED CERCI OF SHORT OR MODERATE LENGTH: AN OVIPOSITOR GENERALLY PRESENT. METAMORPHOSIS SLIGHT OR WANTING.

The Orthoptera form an order of more especially terrestrial insects and many possess greatly developed powers of running or leaping. Except in certain Acridiidæ, flight is not one of their striking characteristics, and alary organs are often abortive or totally wanting. It is noteworthy that the numerous flightless species are not restricted to any particular division of the order, but occur in all the families. Among the exceptional Orthoptera, perhaps the most interesting are the few which have adopted aquatic habits They include several species of Blattidæ and Acridiidæ and one of the Gryllidæ, but these insects do not exhibit any very striking modifications in accordance with their mode of life. In the case of the Blattidæ (vide Shelford, *Zoologist*, 1907) they are able to undergo voluntary submergence and rest with the apex of the abdomen in communication with the air, but are not in any way structurally different from terrestrial species. The aquatic Acridiidæ belong to the Tetriginæ (*Scelimena*) and these insects have the hind tibiæ and tarsi dilated for swimming. They readily take to the water and are good divers (Green, *Ent. Month. Mag.* 1902). The aquatic Gryllid *Hydropedeticus* (Miall and Gilson, *Trans. Ent. Soc.* 1902) is extremely active and skates on the surface of streams in Fiji.

Orthoptera are insects of comparatively large size—very small species are infrequent, while some members of the order are among the largest of existing insects. The number of recorded species is approximately 20,000 and about 500 inhabit Europe. In Britain there are only thirty-one indigenous forms, while eight others are immigrants, which have become naturalized and regularly breed here. In addition to these, there are a number of casual species which have not secured a permanent footing in our islands.

External Anatomy.—The general structure of *Blatta* is described in the work by Miall and Denny (1886) and either this genus or *Periplaneta* is extensively used in zoological laboratories as the introductory type exemplifying insect morphology. Since the Blattidæ are the most generalized of the Orthoptera, a study of a typical member of that family forms an adequate basis for a more extended acquaintance with the order.

The *head*, excepting for variations in size and form, exhibits a remarkable uniformity of general organization. The *Y-shaped epicranial suture* is well seen, for example, in *Blatta* (Fig. 4) and *Gryllus*: in *Mantis* and *Tetrix*, on the other hand, the anterior arms are reduced and evanescent. The *compound* *eyes* attain their greatest size in the Mantidæ, while in the Blattidæ they are markedly reniform: they are usually surrounded by narrow band-like *ocular sclerites* which are well exhibited in *Blatta, Mantis* and *Melanoplus.* The typical number of *ocelli* is three, but these organs are frequently wanting in the Tettigoniidæ and Phasmidæ, while they are variable in the Blattidæ and Gryllidæ. Among the Blattidæ, they are best developed in the winged forms, and exhibit a tendency to disappear in species in which the wings are abbreviated or absent. In *Blatta* there is no median ocellus, and the lateral ocelli are represented by a pair of pale-coloured areas, often referred to as fenestræ. In *Mantis* the ocelli are distinctly larger in the males than in the females. The *frons* is always well developed, and the fronto-clypeal suture rarely wanting: both clypeus and labrum are large. The *antennæ* are typically long, setaceous appendages composed of many joints: in the Acridiidæ, however, they are shorter than the body, and may be more or less clubbed or ensiform, while in the males of some Mantidæ they are pectinated. Band-like *antennal sclerites* are to be seen in many members of the order. The mouth-parts (Figs. 8 and 242) have been studied in detail by Bugnion (1920), Mangan (1908) and Yuasa (1920). The *mandibles* do not call for any detailed mention, they frequently articulate with the head through the intervention of a small basal sclerite on either side—the *trochantin of the mandible*; a prostheca is present in *Blatta* and *Periplaneta* but is not of common occurrence. The *maxillæ* are of the generalized type already described (p. 19). The galea is 2-jointed, a subgalea is generally present, and the cardo is divided into two sclerites: the maxillary palpi are uniformly 5-jointed. The *labium* is characteristically primitive, and the palpi are 3-jointed: the prementum generally exhibits clear evidences of its paired origin, and each division carries a glossa and paraglossa. In certain Acridiidæ (*Melanoplus*) the glossæ are exceptional on account of their extreme reduction (Fig. 242). The *hypopharynx* is large and well developed, and small lateral chitinizations are present which have been regarded as vestigeal superlinguæ. The cervicum is characterized by three pairs of *cervical sclerites* (Fig. 28). The most striking feature in the *thorax* is the large shield-like pronotum which also extensively overlaps the pleura on either side. In certain of the Acridiidæ the pronotum is divided by means of transverse sulci into four areas: the latter, however, are evidently not homologous with the tergites of the remaining thoracic segments which are developed in conformity with the requirements of flight. The meso- and meta- thorax are very much alike, and often structurally identical: according to Snodgrass, the postnotum is wanting from both those segments. The legs (Figs. 20 and 22) differ very much in character among the different families, and their modifications are referred to under the latter. In a broad sense Orthoptera are divisible into those which run or walk (Cursoria) and those which leap (Saltatoria). In the first mentioned division the three pairs of legs are very similar and the tarsi are 5-jointed. In the Saltatoria the hind-legs often attain a great length with the femora swollen proximally: the tarsal joints vary in number and are

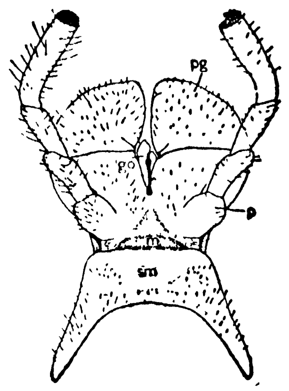

FIG. 242.—LABIUM OF *MELANOPLUS DIFFERENTIALIS*, VENTRAL ASPECT.

pg, paraglossa; *go*, glossa; *p*, palpiger; *m*, mentum; *sm*, submentum. *After* Yuasa, *Journ. Morph.* 33.

always fewer than five. Among other features, the broad flattened coxæ of the Blattidæ, and the presence of a meron in relation with the middle and hind pairs, may be mentioned: the prehensile fore-legs of the Mantidæ, and the highly specialized fossorial anterior limbs of the Gryllotalpinæ are also noteworthy.

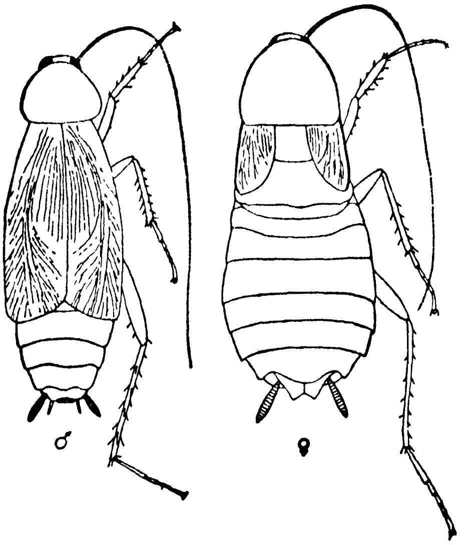

FIG. 243.—*BLATTA ORIENTALIS*, SLIGHTLY ENLARGED.

√The anterior pair of *wings* are usually referred to as tegmina: they are somewhat hardened and parchment-like in consistency, a feature which enables them to serve as shields for the more delicate membranous hind-wings. The latter are characterized by the great development of the anal area which may occupy the major portion of the wing. When at rest, the left tegmen usually slightly overlaps the right one, and the wings are folded in a longitudinal manner beneath them. The degree of development of the alary organs presents many variations throughout the order. As a rule, the tegmina are elongate and relatively narrow, but they may be reduced to mere scales as in many Phasmidæ. In other cases, both pairs of wings may be so reduced as to be useless for flight, as, for example, in the female of *Blatta orientalis* (Fig. 243). In some genera the bases of the tegmina only persist as stridulatory areas, and there are, furthermore, a large number of species entirely devoid of alary organs. The development of the wing veins merits much fuller investigation than has hitherto been accorded to it. In some Blattidæ the wing tracheæ clearly approach very closely to the primitive hypothetical type since the basal transverse trachea is not developed. According to Comstock and Needham the costal trachea is wanting or vestigeal: Sc is well developed and both it and R often give off many supernumerary branches towards the anterior margin of the wing. This development of accessory veins is characteristic of the order, and a large number are present to give support to the extensive anal area of the hind-wing. The venation (Figs. 244, 245) as a whole is of a generalized type and, with the exception of C, all the primary veins are repre-

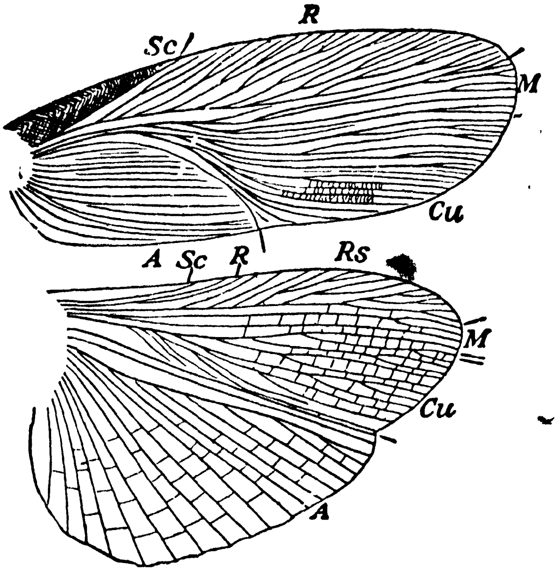

FIG. 244.—RIGHT WINGS OF *PERIPLANETA AUSTRALASIÆ*.

Adapted from Handlirsch.

sented: a common feature is the frequent reduction of Rs and M. Although well developed cross-veins are present, the spaces between the veins are frequently occupied by an irregular network, which is a survival of the primordial archedictyon.

The *abdomen* consists of ten evident segments which are represented by their terga, while vestiges of an eleventh segment are to be found in the suranal and podical plates. On the ventral aspect, the first sternum is wanting or much reduced; sterna 2 to 9 are to be observed in the males, and the 10th sternum is vestigial or absent in the adults of both sexes. In the females of *Blatta* the last visible sternum is the 7th, and the 8th and 9th sterna are telescoped into it to form the genital pouch. A more primitive condition is exhibited in *Gryllotalpa* where the genital pouch is not developed: in this insect the 8th and 9th sterna are externally visible, the last mentioned plate being represented by a pair of small shields. In the males, the 9th sternum bears a pair of anal styli: the latter organs are present in the nymphs of both sexes but in *Blatta*, for example, they disappear in the female after the fifth ecdysis.

Cerci are generally present and vary greatly among different families. These organs are long and 8-jointed in *Grylloblatta*; short and 16-jointed in *Blatta*; very long and unjointed in the Gryllidæ and reduced to small processes in the Acridiidæ. An exserted ovipositor is well developed in *Grylloblatta* (Fig. 247) which in this respect is unique among the Cursoria: it is also present in almost all Saltatoria. In the Blattidæ, Mantidæ, and Phasmidæ it has undergone great reduction and is not evident without dissection. When completely developed the ovipositor consists of three pairs of gonapophyses of which the outer pair forms the long blades in *Grylloblatta* and Tettigoniidæ; the middle, or inner, pair is composed of slender processes, which fit in grooves situated on the first or lower pair of gonapophyses (Fig. 45). In *Acridium* all the parts are very short and the inner gonapophyses minute: in *Blatta* there are similarly three pairs of reduced genitalia, which are concealed in the genital pouch.

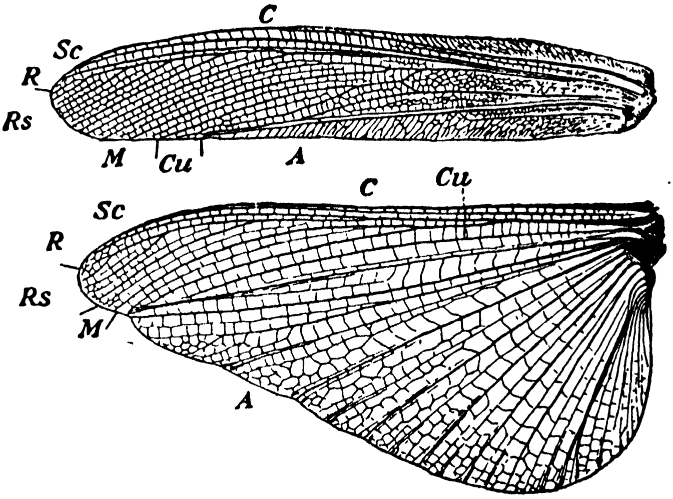

FIG. 245.—RIGHT WINGS OF *SCHISTOCERCA*.
Adapted from Handlirsch after Brongniart.

One of the most characteristic features of the Saltatoria are the *stridulatory organs* and, with very few exceptions, it is the males alone which are capable of sound production. These organs are of two principal types: (*a*) the alary and (*b*) the femoro-alary. The first type is seen in the Gryllidæ and Locustidæ. In *Gryllus* each tegmen bears a rasping organ or *file* and a hardened area or *scraper*, the file of the one tegmen working against the scraper of the other. In the Tettigoniidæ on the other hand this two-fold or ambidextrous arrangement is no longer maintained. The file is only functional on the left tegmen and the scraper on the right one. In the Acridiid subfamily Œdopodinæ stridulation is produced by the friction of the upper surface of the costal margin of the wings against the lower surface of the thickened veins on the tegmina. Femoro-alary stridulatory organs are characteristic of the remainder of the Acridiidæ. Sound is produced by rubbing the inner aspect of the hind femora, upon each of which there is a row of projecting pegs, against the thickened basal area of the radius of each tegmen. *Auditory organs* (vide p. 91) are present in all sound-producing species. Whatever the type may be, each organ consists of a thin cuticular membrane, or tympanum, whose vibrations are transmitted to the sensory centres by means of scolopalæ, which are connected with the nerve endings. In the Acridiidæ the auditory organs are highly specialized, and their tympanal portions are seen one on either side of the first abdominal segment. In Tettigoniidæ and Gryllidæ these organs are different in type and consist of a pair of tympana situated near the proximal end of each fore-tibia. In many genera these tympana are freely exposed but, in some cases, they are largely concealed. In the latter event each is covered by an integumental fold, so that it comes to lie in a cavity, which only communicates with the exterior by means of an elongate slit-like opening.

Internal Anatomy.—The principal features of the *digestive system* (Figs. 108,111) are the presence or absence of convolutions and of enteric cœca, the number and disposition of the Malpighian tubes, and the form and internal structure of the gizzard. As a general rule the œsophagus expands into a capacious crop, which is succeeded by an elaborately developed gizzard. The mid-intestine is variable in length and frequently convoluted: except in the Phasmidæ, there are two to eight enteric cœca. The Malpighian tubes are numerous (circa 30–120) and filiform, and in the hind intestine there are six rectal papillæ. Salivary glands are, in general, well developed and lobulated (Fig. 154), each lobe consisting of groups of glandular acini (vide Hofer, 1887): salivary reservoirs are also present in the majority of species. The detailed structure of the digestive system has been very fully investigated by Bordas (1898) in a number of species and its characteristics in different families are as follows.

Phasmidæ.—Alimentary canal without any convolutions, the gizzard atrophied and no enteric cœca. The anterior portion of the mid-intestine with thick circular muscle bands: the posterior region with numerous superficial glandular papillæ and drawn out terminally into filaments. Malpighian tubes grouped in bundles opening at the summits of tubercles.

Blattidæ.—Alimentary canal long and sinuous, the crop voluminous and the gizzard provided with a powerful masticatory armature. Eight tubular enteric cœca; Malpighian tubes arranged in six groups (Fig.108).

Mantidæ.—Alimentary canal either straight or sinuous, the crop well developed, and the gizzard rudimentary. Eight tubular enteric cœca and voluminous salivary glands.

Acridiidæ.—Alimentary canal straight, the crop large and the gizzard wanting or vestigeal. The mid-intestine longitudinally plaited; six enteric cœca each provided with a short posterior diverticulum. Malpighian tubes disposed in bundles and salivary glands rudimentary.

Tettigoniidæ.—Alimentary canal long and convoluted, the crop well developed, the gizzard voluminous and provided with a very powerful internal armature of teeth disposed in six ridges. Two sac-like enteric cœca embracing the gizzard laterally. Malpighian tubes capillary, opening in groups at the summits of small papillæ.

Gryllidæ.—The alimentary canal long and convoluted: the crop and gizzard large, the latter with a strong chitinous armature. The enteric cœca as in Locustidæ: Malpighian tubes arranged in a single bundle discharging into the extremity of a common duct or ureter (Fig.108).

The *nervous system* is of a generalized character and in addition to the cephalic centres there are three thoracic and five or six abdominal ganglia. *Gryllotalpa* in exceptional, and according to Newport, in addition to those of the thorax, there are only four ganglia in the abdomen. The longitudinal connectives are double throughout the length of the ventral cord: they are usually widely separated in the thorax and closely approximated, although distinct, in the abdomen. The brain has been studied by Packard in *Melanoplus* and its histology has been investigated by Newton (*Q.J.M.S.* 1879) in *Blatta* and by Viallanes (1888) in the Acridiidæ. This organ exhibits a greater structural simplicity in the last mentioned family than in either the Blattidæ or Gryllidæ. In the two latter families the mushroom bodies are better developed and, in the Blattidæ, the calyces are double and relatively complex. The sympathetic system is well developed in Orthoptera and has been investigated by Hofer (1887). The *tracheal system* (Fig. 127) communicates with the exterior by means of ten pairs of spiracles, the first two being thoracic and the remainder abdominal in position. In certain of the Acridiidæ there is a highly-developed system of air-sacs which exhibit a segmental disposition: one very large pair is situated in the prothorax and there are five pairs of abdominal sacs. In addition to these principal vesicles, which are superficial in position, a large number of smaller sacs are distributed among the muscles (Packard). The *circulatory system* has been described by Miall and Denny in *Blatta*. The heart (Fig. 133) consists of thirteen chambers, which correspond with each of the thoracic and ten abdominal segments: there are twelve pairs of alary muscles and these are inserted into the pericardial diaphragm. The female *reproductive system* of *Periplaneta* (vide Bordas, 1909) consists of a pair of ovaries each composed of eight panoistic ovarioles (Fig. 162). The two oviducts combine to form a common vagina which opens into the genital pouch (vide p. 237) by a median pore on the 8th sternum. A pair of branched colleterial glands open into the vagina on its ventral aspect. The left gland is larger than the right one and secretes a quantity of carbonate of lime: the right gland secretes a viscid substance and the products of the two glands are utilized in the formation of the ootheca. The spermatheca consists of two vesicles of unequal size opening on the 9th sternum, which forms the dorsal wall of the genital pouch. Among other Orthoptera there is a considerable variation in the number of ovarioles: thus in *Acrida turrita* there are 16 to each ovary and in Tettigoniidæ they are very numerous. The colleterial glands attain their greatest development in the Blattidæ and Mantidæ, which produce highly developed oothecæ. In the last mentioned family there are two pairs of these glands and in the Gryllidæ they are represented by mucous glands. Among Tettigoniidæ and Acridiidæ colleterial glands are wanting: in the former group there is a tubular diverticulum ("boyau" of Fenard) of the vagina, and in the Acridiidæ a somewhat similar outgrowth arises from the apex of each oviduct. In these cases the diverticula provide a mucilaginous secretion which is applied to the eggs and in the Acridiidæ it unites them into a common mass. A spermatheca is of general occurrence among Orthoptera but is exceedingly variable in character. In *Blatella germanica* it consists of two pairs of sacs while among Tettigoniidæ it is a single organ. The seminal duct, moreover, may be exceedingly short as in *Blatta*, long as in *Gryllotalpa*, or complexly coiled as in many Acridiidæ.

The *male reproductive organs* of *Periplaneta* (Fig. 158) are described by Miall and Denny. The testes lie in the 5th and 6th abdominal segments and each consists of 30–40 rounded vesicles which are arranged in longitudinal series along the apical portion of the vas deferens. The vasa deferentia discharge into the vesiculæ seminales which are sac-like enlargements at the anterior extremity of the ejaculatory duct. They are concealed by the greatly developed accessory glands; the latter consist of two series of tubules arising from the walls of the vesiculæ and from the anterior portion of the ejaculatory duct. Collectively, the accessory glands form a large compact mass which was termed by Huxley "the mushroom-shaped gland." Situated beneath the ejaculatory duct there is an unpaired gland (conglobate gland of Miall and Denny) which opens separately upon a forked sclerite forming part of the genitalia. According to Bordas it is an odoriferous gland of defensive function, which secretes a volatile alkaline fluid and is comparable with the pygidial glands of Coleoptera. Among other Orthoptera there is great variation in the form and structure of the testes; accessory glands are generally present, and vesiculæ seminales are of two types. In *Gryllus campestris* and *Œcanthus* the latter organs are formed as convoluted enlargements of the vasa deferentia, while in the Mantidæ and in *Gryllotalpa* they are cœcal outgrowths which open directly into the ejaculatory duct. For more detailed information with regard to the reproductive organs in both sexes of Orthoptera reference should be made to the paper of Fenard (1896).

In addition to the glands associated with the alimentary canal and reproductive system there are, in many Blattidæ, *repugnatorial glands* which are situated beneath the abdominal terga. In *Blatta orientalis* they take the form of two pouch-like invaginations of the body-wall between the 5th and 6th terga in both sexes. In *Blattella germanica* these glands are extensive in the male and reach far into the body-space, while they are wanting in the female (Minchin, *Q.J.M.S.* 1888; *Zool. Anz.* 1890). A sternal gland opening between the 6th and 7th sterna is also present in *B. orientalis* (Harrison, *Q.J.M.S.* 1906). *Mandibular glands* have been found by Bordas in the Mantidæ and dorsal *prothoracic glands* occur in the latter family and in the Phasmidæ. In the males of *Œcanthus* there is a large *metanotal gland* which is indicated externally by a deep depression on the metatergum. According to Fulton (1915) the gland opens to the exterior by means of two pairs of pores. The latter are connected with much branched tubuli which extend back into the abdominal cavity. The function of this evidently important organ is not fully understood, but it is believed to be an alluring gland whose secretion is attractive to the female during copulation.

Post-embryonic Growth.—The eggs of Orthoptera are more or less cylindrical and in the Blattidæ and Mantidæ they are deposited in oothecæ: in the Phasmidæ each egg is enclosed in a separate seed-like capsule (Fig. 246). Among the Acridiidæ, although there is no true ootheca, a secretion of the colleterial glands is poured out which hardens around the eggs, uniting the latter into a single compact mass. Among many Orthoptera, notably in the Mantidæ, Acridiidæ and in *Œcanthus* the young insect sheds a membranous covering shortly after emergence from the egg. The insect frees itself from this investment by convulsive movements of the body aided by pressure exerted by the cervical ampulla described below. This covering has frequently been regarded as the amnion but, in so far as the Mantidæ are concerned, Williams and Buxton (1916) have shown that it is a true nymphal cuticle, separately enveloping the antennæ and limbs, and that the shedding of it constitutes the first ecdysis. An amnion, on the other hand, encloses the insect as a whole in the form of a sac and does not envelop the appendages separately. In *Blatta* an ecdysis is also stated to occur shortly after emergence but this feature is difficult to observe owing to the readiness with which the nymphs devour their exuviæ. The number of ecdyses which occur during the life of an Orthopteron is subject to great variation, not only in different families but also among the individuals of a single species. Five ecdyses are recorded for example in *Œcanthus* and *Melanoplus*, six in *Blatta* and from three to twelve in the Mantidæ. In many Orthoptera the soft cervical membrane plays an important part during ecdysis: it is capable of being distended, by the influx of blood, into a swollen dorsal ampulla which protrudes immediately behind the head. According to Herculais (*Bull. Soc. Ent. Fr.* 1890) in *Stauronotus* a turgid condition is maintained by the accumulation of air in the crop which lies beneath the ampulla and, by means of the pressure thus exerted, the insect is able to rupture the old cuticle. This observer also mentions that the cervical ampulla plays an important part in the escape of the insects from the capsule which encloses the eggs. Six or seven young insects combine their efforts and force open the lid of the capsule by means of their ampullæ, and thereby effect their exit.

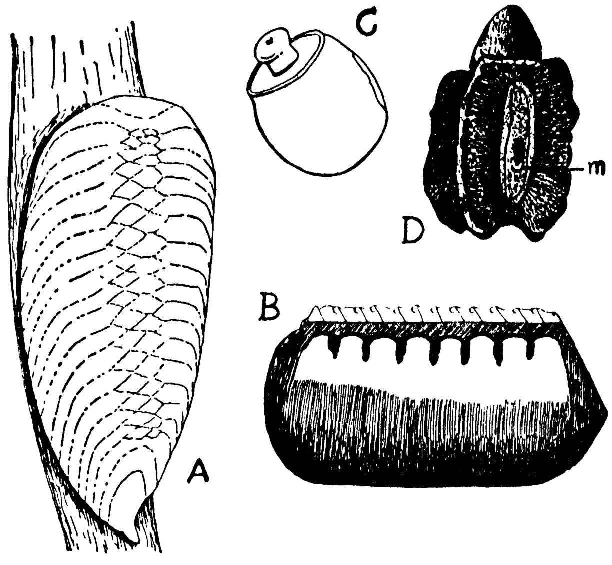

Fig. 246.—Oothecæ. A, *Mantis*. B, *Blatta orientalis* (after Miall and Denny). C, *Carausius morosus* (after Ling Roth). D, *Phyllium crurifolium*, *m*, Micropyle (after Henneguy). All enlarged.

In the apterous members of the order post-embryonic growth consists merely of an increase in size, and in the further differentiation of the appendages and genital segments: in other words metamorphosis is absent and the young closely resemble their parents. In the winged forms a slight but gradual metamorphosis is evident, and the rudiments of alary organs are usually evident in the third instar. In *Melanoplus* and *Œcanthus*, which pass through six nymphal instars, the wing rudiments appear as slight extensions of the meso- and meta-nota in the second instar, becoming clearly evident after the subsequent ecdysis. The position assumed by the wings in the saltatorial Orthoptera during their nymphal instars is different from that found in the adults. In the immature forms the wings have undergone torsion with the result that their surfaces and margins are inverted and in positions which are the opposite to those assumed in the perfect insects.

Literature on Orthoptera.—The most important monographs on the European members of the order are those of Brunner von Wattenwyl (1882) and of Tumpel (1922). The first mentioned authority (1893) has also published a comprehensive work on most of the families and genera, and Kirby (1904–10) has catalogued the species of the world. Burr (1910) has written a short synopsis of the species of western Europe, Chopard has monographed the French species, and the British forms have recently been the subject of a volume by Lucas (1920). The best general summary of our knowledge of the Orthoptera is given by Sharp (*Ins.* pt. 1) : a good deal of information will also be found in the work of Blatchley (1920). Among other contributions those of Miall and Denny (1886) on the cockroach and Packard (1875) on the Rocky Mountain locust may be mentioned. Among writings devoted to special families those of Brunner and Redtenbacher (1906–08) on the Phasmidæ ; Westwood (1889) on the Mantidæ ; the contributions to " Genera Insectorum " by Shelford on the Blattidæ, and by Caudell, Bolivar and others on the Acridiidæ and Tettigoniidæ, are important.

Classification.—The original name applied to the order by De Geer was Dermaptera and this was subsequently replaced by the term Orthoptera which is due to Oliver, There is a tendency among modern students to divide the Orthoptera into several distinct orders restricting the original name to the saltatorial forms only. This course appears scarcely to be warranted and is largely due to differences of opinion with reference to characters which are to be regarded as of ordinal value. In the present work eight families are recognized which may be identified with the aid of the following synopsis :

1 (8).—Legs usually of approximately equal size, the hind-femora not adapted for leaping ; tarsi 5-jointed. Sound-producing organs absent. Ovipositor almost always concealed. **Cursoria**

2 (3).—Apterous ; ovipositor exserted, cerci long. GRYLLOBLATTIDÆ (p. 242)

3 (2).—Winged or apterous ; ovipositor concealed and often rudimentary, cerci short.

4 (5).—Pronotum large and shield-like ; coxæ very broad, protecting lower surface of body. BLATTIDÆ (p. 243)

5 (4).—Not as in 4.

6 (7).—Fore-legs highly modified for raptorial purposes ; prothorax generally very long. Eyes large, ocelli 3. Cerci jointed. MANTIDÆ (p. 244)

7 (6).—Fore-legs normal ; mesothorax very long. Eyes small, ocelli usually absent. Cerci unjointed. PHASMIDÆ. (p. 245)

8 (1).—Legs of unequal size, the hind-femora enlarged for leaping ; tarsi with fewer than five joints. Sound producing organs present. Ovipositor generally exserted. **Saltatoria**

9 (10).—Antennæ shorter than body ; tarsi usually 3-jointed. Stridulatory organs on tegmina and hind-femora ; auditory organs at base of abdomen. Ovipositor short. ACRIDIIDÆ (p. 246)

10 (9).—Antennæ filiform, often longer than body ; tarsi usually 3- or 4-jointed. Stridulatory organs on tegmina only : auditory organs on fore-tibiæ. Ovipositor long.

11 (12).—Tarsi 4-jointed, ovipositor ensiform. TETTIGONIIDÆ (p. 248)

12 (11).—Tarsi 3-jointed (rarely 1- or 2-jointed or wanting), ovipositor usually cylindrical and acicular.

13 (14).—Ovipositor acicular, hind-femora enlarged. Most GRYLLIDÆ (p. 249)

14 (13).—Ovipositor concealed, hind-femora scarcely enlarged, fore-legs strongly fossorial. GRYLLIDÆ part (p. 250)

FAM. GRYLLOBLATTIDÆ.—This family is represented by four species of *Grylloblatta* Walk. from western N. America and Japan. The best known is *G. campodeiformis* Walk., which is an apterous thysanuriform insect found among stones, etc., in the Rocky Mountains at an altitude of about 6,500 ft. Structurally it is a very generalized type combining certain Gryllid and Blattid features with those found in the Dermaptera, Isoptera and Plecoptera. The eyes are small and there are no ocelli; the antennæ are long and filiform and the tarsi are 5-jointed. The females possess an exserted sword-like ovipositor similar to that found in Tettigoniidæ and differ thereby from all other cursorial Orthoptera: combined with this feature is the presence of long 8-jointed cerci (Fig. 247). For further information on this family reference should be made to papers by Walker (1914,–19,–31,–33).

FAM. BLATTIDÆ. (Cockroaches).—The Blattidæ are eminently tropical insects and, although abundantly represented in individuals, the number of species inhabiting temperate zones is relatively small. Most of what is known concerning these insects has been derived from a study of certain forms which have become naturalized in various parts of the world. They are readily transported in the holds of ships from one country to another, and afterwards become disseminated through merchandise. Blattidæ are very swift runners, and the legs are all very much alike: their large broad coxæ cover the ventral surface of the thorax and the base of the abdomen. The head, when in repose, is reflexed beneath the thorax; the antennæ are very long, filiform, and often consist of nearly one hundred joints. The eyes are large and reniform, a pair of ocelli are usually present in the winged forms; when the alary organs are abbreviated or wanting, ocelli are often represented by pale spots (fenestræ). The pronotum is large and broad, often concealing the head: the meso- and meta-thorax are smaller and sub-equal in size. The tegmina and wings exhibit many variations in length compared with that of the abdomen: in some genera (*Blattella* and *Periplaneta*) they completely cover the latter region while in others (males of *Blatta*) they leave the distal portion of the abdomen exposed (Fig. 243). Very frequently the alary organs are abbreviated in the female, as in *Blatta*, or absent as in *Polyphaga* and its allies. When fully developed, the wings are characterized by the great development of the anal area which in repose is folded longitudinally like a fan, and often comprises more than half of the wing. The abdomen carries a pair of jointed cerci and there are generally also anal styli in the males. Although cockroaches are usually of a testaceous or dark mahogany hue there are tropical species which exhibit both elegance of form and beauty of coloration.

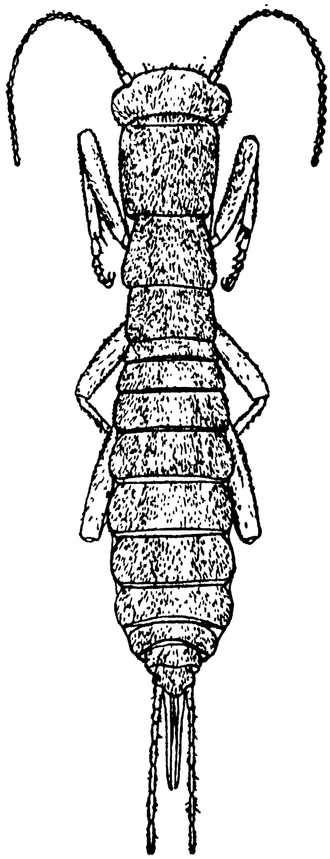

FIG. 247.—*GRYLLOBLATTA*, FEMALE. *After* Walker, *Can. Ent.* 1914.

The domesticated species are omnivorous and, although they exhibit a partiality for sweetened or starchy matter of various kinds, they are known to feed upon a great variety of substances including provisions, paper, clothing, books, shoes, etc., and also dead insects. As a rule they injure and soil far more of different substances than they consume. Comparatively little is known with regard to the natural food of the indigenous species of different countries: Brunner considered that it consists largely of dead animal matter. About 1,200 species of cockroaches are known and they occur naturally under dead leaves, moss, refuse, and on flowers and bushes, In Great Britain there are two indigenous species belonging to the genus *Ectobius*, which live out of doors among the undergrowth of woods or on the seashore. There are also five naturalized aliens of cosmopolitan range: these regularly breed in Britain although not under natural conditions. In addition to the foregoing, about twenty species have occurred casually (*vide* Lucas, 1920). Of the naturalized or domesticated species there are two which frequent buildings, viz. the common or oriental cockroach *Blatta orientalis* and the rarer German cockroach *Blattella germanica*. Occasionally three other species are found in warehouses or hothouses, viz. *Periplaneta americana*, *P. australasiæ* and *Leucophæa surinamensis*.

The eggs of Blattidæ are commonly laid in horny purse-like oothecæ (Fig. 246): these capsules are very similar in structure but vary in size and shape, and in the number of eggs they contain, in different species: in *Blatta orientalis* there are sixteen eggs to a capsule and in *Blattella germanica* they average about forty. The ootheca is divided longitudinally by a membranous partition into two chambers. Within each of the latter there is a row of cylindrical pockets and a single egg is lodged in each pocket The ootheca is formed in the genital pouch of the female and the eggs descend singly from alternate ovaries: the pouch is increased by additions to its substance and its first formed portion soon begins to protrude from the body. When the full number of eggs have entered it, the ootheca is closed and, after being carried about for a variable time projecting from the body of the female, it is deposited in some suitable crevice. In some species the ootheca is reduced to a thin transparent investment, and it may be retained within the brood pouch of the female, the latter being viviparous: in other instances an ootheca is not constructed at all. In normal conditions, when the nymphs are ready to emerge, the ootheca splits along its dorsal edge, the two halves extend apart and the young struggle out. In *Blatta orientalis* there are said to be six, or possibly seven, ecdyses and the whole period occupied in development from the egg to the adult is stated to occupy about a year (Rau, *Trans. Acad. Sci. St. Louis*, 1924). *Blattella germanica*, on the other hand, completes its development in considerably less than a year.

FAM. MANTIDÆ (Praying Insects).—This extensive family is composed of exclusively carnivorous species and occurs in all parts of the world, excepting the cooler regions. Its members are easily recognized by the peculiar form of the front legs, which are adapted for seizing and retaining the animals which form their prey. Each fore-coxa is much elongated, and the femur bears, on the ventral aspect, a groove which is armed along its two edges with a series of spines. The tibia is adapted to close in this groove after the manner of the blade of a pocket-knife, its sharp toothed edge serving to firmly retain the prey, the teeth fitting in between those of the femur (Fig. 248). Armed in this way, the mantis often sits motionless for long periods at a time, with the head upraised upon the elongate and sub-erect prothorax. The powerful raptorial fore-legs are raised together in front, their pincers being partially opened to seize any suitable prey that ventures within range. This curious attitude, which suggests one of supplication, has earned for its possessors the name of "praying insects." Many legends and superstitions are associated with the species *Mantis religiosa*: the ancient Greeks endowed it with supernatural powers: some of the Moslem peoples maintain that it prays with its face turned towards Mecca: in other countries it is regarded as a saint, mendicant or soothsayer and in Andalusia it is known as "Santa Teresa." Notwithstanding these attributes, mantids are veritable tigers of the insect world, and feed voraciously upon flies, grasshoppers, caterpillars, etc. They are very pugnacious, the larger forms often devouring the smaller, and females the males. Some of the large S. American species have been recorded as even attacking small birds, lizards and frogs. Mantids are extremely variable in form, and are assimilated in a remarkable manner to their surroundings more especially, it would appear, in order to deceive their prey rather than to protect themselves. The green colour of the typical mantis serves this purpose admirably: those that simulate flowers have the advantage of attracting flower-haunting insects within their reach. Certain tropical species possess foliaceous expansions on the prothorax and limbs, while *Pyrgomantis* is so attenuated as to resemble a Phasmid.

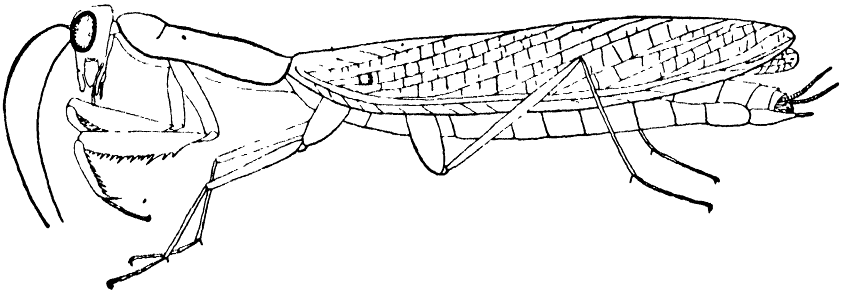

Fig. 248.—*Mantis religiosa*, Male. S. Europe.

The head in the Mantidæ is extremely mobile and is connected with the prothorax by means of a slender neck. The eyes are very large: in some forms they assume curious shapes, and may be elongate and horn-like. There are three ocelli and these organs are rarely wanting. The prothorax is almost always longer than any other trunk segment, and may even exceed in length the whole of the after-body. Both the middle and hind pairs of legs are slender and weakly developed, the insects moving in a slow and ungainly manner. The tegmina frequently have very much the appearance of foliage, particularly in the females, but the alary organs in the latter sex are but little adapted for flight. The abdomen is terminated by short jointed cerci, an exserted ovipositor is wanting, and there is a pair of anal styli in the male.

The eggs of Mantidæ are laid in oothecæ (Fig. 246) which are attached to twigs, bark, walls and other objects. Each female makes four or five of these cases and their type of construction varies in different species. In the Indian *Gongylus*, for example, Williams (*Trans. Ent. Soc.* 1904) states that the ootheca consists of an outer covering formed of a more or less frothy secretion which hardens into a firm spongy substance. Within this envelope is a layer of about forty egg-chambers arranged four abreast : they are constructed of a viscid material which very rapidly hardens to the consistency of horn. In the Chinese *Hierodula saussurii* Kershaw (*Psyche,* 1910) mentions that the oothecæ are about an inch long, and the egg-chambers number about twenty-four, arranged in two longitudinal rows. An air space is left between the layer of eggs and the outer covering, and the latter is composed of overlapping strips of extremely hard, tough material. Other types of oothecæ are described by Shelford (*Trans. Ent. Soc.* 1909) and by Williams and Buxton (*Ibid.* 1916). It would appear that the eggs of Mantidæ are admirably protected by these cases, but the latter are ineffective in warding off the attacks of insect enemies, judging from the frequency with which parasitic Hymenoptera are bred out from them. It is possible, however, that they serve to protect the eggs from birds and lizards. After emergence, the young mantids have been observed to hang suspended from their oothecæ by means of silken threads. The latter are secreted by a pair of papillæ on the 10th sternum but after the first ecdysis silk is no longer produced (Williams and Buxton). The number of ecdyses passed through is not constant and from accounts given by different observers it varies between three and twelve. The whole life-cycle occupies about a year. More than a dozen species occur in western Europe, of which the most familiar is *Mantis religiosa.* This insect ranges as far north as central France and has been introduced by means of nursery stock into N. America where it has become locally established.

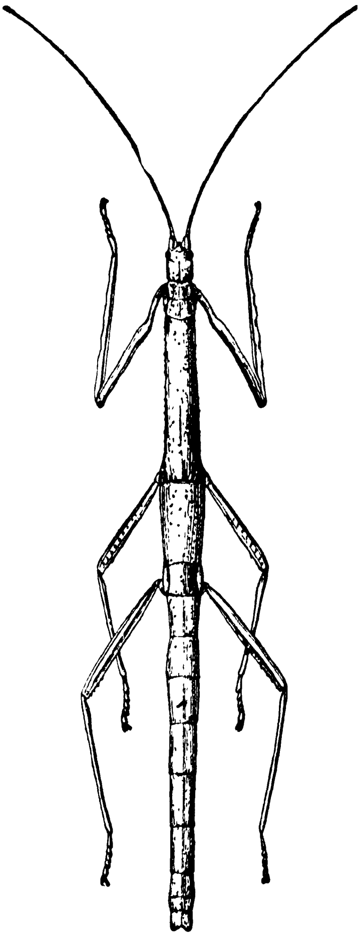

FIG. 249.—*CARAUSIUS MOROSUS*, NAT. SIZE. *After* Ling Roth.

FAM. PHASMIDÆ (Stick Insects, Leaf Insects).—These insects are among the most curiously modified of all Orthoptera. Some of the linear forms attain a length of nine and even thirteen inches (33 cm.) and are the longest, although by no means the bulkiest, of living insects. Many closely simulate sticks or grass stems and when at rest, or feigning death, they are among the most difficult of all insects to detect in the field (Fig. 249). Others (Phyllinæ) have broad lamina-like bodies with membranous expansions to the legs and closely resemble leaves both in form and coloration. A certain number of species are invested with spiny outgrowths and some resemble pieces of lichen-covered bark. As a rule the plant-like appearance is most developed in the female. Phasmids have a characteristically elongate meso-thorax, the pro-thorax is small, and the three pairs of legs differ little from one another. The cerci are short and single-jointed, styli are wanting and the short ovipositor is concealed by the subgenital plate. The tegmina are generally small, often scalelike, or wanting even in cases where the wings are well developed. In many species there are no alary organs at all. The sexes are frequently very dissimilar, the male being small, rather active and winged, and the female large, sluggish, and apterous. All the species are vegetable feeders and extremely voracious, although they are rarely sufficiently abundant to cause appreciable injury to economic plants. They are essentially denizens of tropical and subtropical countries and over 700 species are known. Two genera are European while *Bacillus gallicus* is the only species which ranges as far north as central France. The number of eggs laid by these insects is commonly stated to be very small, but it is noteworthy that Ling Roth found the average number laid by *Carausius morosus* was 480 with a maximum of 712, the period of oviposition extending over about 225 days. The eggs are dropped from the plants upon which the insects are resting and the incubation period is a lengthy one: in some species they may remain on the ground for nearly two years before hatching. Each egg is enclosed in a separate hard capsule, and the latter is provided with an operculum which allows of the exit of the young insect. These capsules are variously and often very remarkably sculptured, and bear an extremely close resemblance to seeds (Fig. 246). The biology of the family has been studied by Sinety (1901) and the growth and habits of *Carausius morosus* have been investigated in great detail by Ling Roth (*Trans. Ent. Soc.* 1917) and Talbot (*Ibid.* 1920). Post-embryonic growth is slow, and the life-cycle in the above-mentioned species occupies more than a year and a half from the time the eggs are laid. In the apterous forms the morphological changes during growth are slight and metamorphosis is almost non-existent. The number of ecdyses passed through is extremely variable, often among individuals of a single species; thus in *C. morosus* Ling Roth records six ecdyses, Sinety five or six, and Talbot three, or rarely four. Parthenogenesis is of frequent occurrence among Phasmids and in some species males are exceedingly rare.

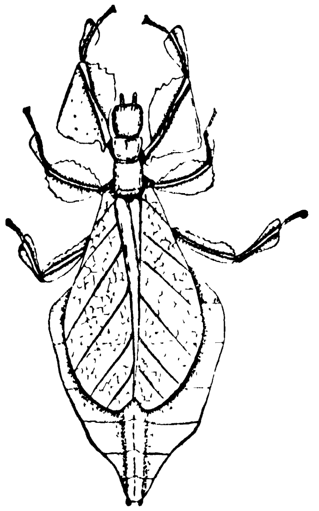

FIG. 250.—*PHYLLIUM CRURIFOLIUM*, HALF NATURAL SIZE. Oriental region.

The Phyllinæ include the leaf-insects which are almost entirely confined to the moister parts of the Oriental region and more especially to the islands of the Indian ocean. Their biology has been less thoroughly studied than in other Phasmids and has been principally observed in *Phyllium crurifolium* by Joly (1871) and others. The sexes differ very remarkably; the males have small tegmina, well developed wings, and relatively narrow bodies. In the female the tegmina are extensive leaf-like expansions, the wings are vestigial, and the body very much expanded (Fig. 250).

FAM. ACRIDIIDÆ (Locusts and Short-horned Grasshoppers).—The Acridiidæ are composed of the common grasshoppers of the country-side, together with the various species of migratory locusts and a number of other more highly specialized forms. The antennæ, with few exceptions, are much shorter than the body and are either filiform, clubbed or ensiform. The stridulatory apparatus is usually formed by a ridge of about eighty to ninety peg-like points along the inner aspect of the hind femora, which are rubbed against the hardened veins (radius) of the closed tegmina, thus causing the latter to vibrate and produce a low buzzing sound (Fig. 102). The males stridulate by day and when at rest, but the females are noiseless: rudimentary organs of a similar kind are found, however, in the females of *Stenobothrus*. Members of the Œdipodinæ are exceptional in that the males stridulate while on the wing, producing their notes by the friction of the upper surface of the costa of the wings, and the under surface of the thickened veins of the tegmina. A crackling sound results which has been compared to that of burning stubble. The auditory organs are located one on each side of the basal segment of the abdomen. The ovipositor is not conspicuous and its valves are short and curved (Fig. 251). By means of the latter organs the female excavates a hole in the ground or more rarely in decaying wood. The eggs are then deposited until they form a mass of 30–100 or more and, during the process, a glutinous fluid is discharged around them which hardens to form a water-proof protection, corresponding to the more perfect oothecæ of the Cursoria (Fig. 246). Several of these masses are usually deposited by each female and the oviposition period in *Caloptenus* extends, according to Riley, over a period of two months. There appear to be five to eight ecdyses in the life of a species and commonly one or two generations in the year. These insects are voracious devourers of vegetation during both their young and adult stages.

The Acridiidæ are divided into nine sub-families of which the Tetriginæ and Truxalinæ are alone represented in the British Isles, their members forming a large part of our meagre fauna of Orthoptera. The Tetriginæ or "grouse locusts" are of a uniform small size and brownish colour, with a remarkably developed pronotum which is produced far back over the body (Fig. 251). They are represented in the British Isles by three species of *Acrydium*, *A. kiefferi* being one of the commonest grasshoppers. In many exotic species of the group the pronotal extension assumes varied and extraordinary forms recalling similar developments in the Membracidæ. The Truxalinæ include the common field grasshoppers and are distributed throughout the globe: the British fauna contains nine species. The Œdipodinæ or band-winged locusts are more or less brightly coloured insects, often with blue, yellow or red wings crossed by a characteristic black fascia. The tegmina, however, are sombrely coloured and when closed the insect harmonizes very closely with its environment. The genus *Locusta* L. (*Pachytylus* Fieb.) includes one of the chief migratory locusts of the Old World. According to Uvarov (*Bull. Ent. Res.* 1921) it comprises only two species, *L. migratoria* and *L. pardalina*. Both species exist in two phases—a destructive migratory one and a solitary harmless one. In the case of the first mentioned species its migratory phase under tropical conditions is the form *migratorioides* but in the palæarctic region it is represented by the form *migratoria* which is intermediate in characters between the former and the solitary form *danica*. This fact is explained by the absence of tropical heat and moisture in its palæarctic breeding grounds. The latter are located in the vast reed-beds in the deltas of the rivers flowing into the Caspian and Aral Seas and Lake Balkash. The effect of the conditions in this region is such that the swarming phase does not reach the extreme differentiation represented by *migratorioides* but stops, half-way as it were, at *migratoria*. When the increase of this locust is at its highest large swarms are formed owing partly to the gregarious instincts exhibited in this phase. Migration from the breeding ground follows, but the causes are not fully understood. The locusts are not driven by hunger, since they do not feed much at that period but exist at the expense of their fat-bodies. The cessation of flight is stated to be due to internal physiological causes, including the maturition of the gonads, and is not connected with the discovery of suitable breeding grounds. The resulting progeny develops into the *danica* phase which, although non-gregarious, aids in the distribution of the species. Given favourable localities this phase gives rise, in its turn, to the migratory one.

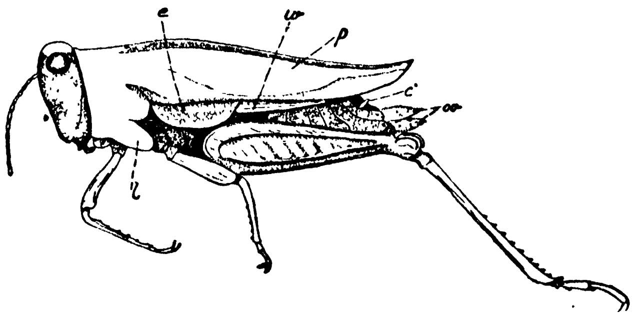

FIG. 251.—ACRYDIUM KIEFFERI × 5. *c*, cercus; *e*, tegmen; *ov*, ovipositor; *p*, pronotum; *l*, lateral lobe; *w*, wing.

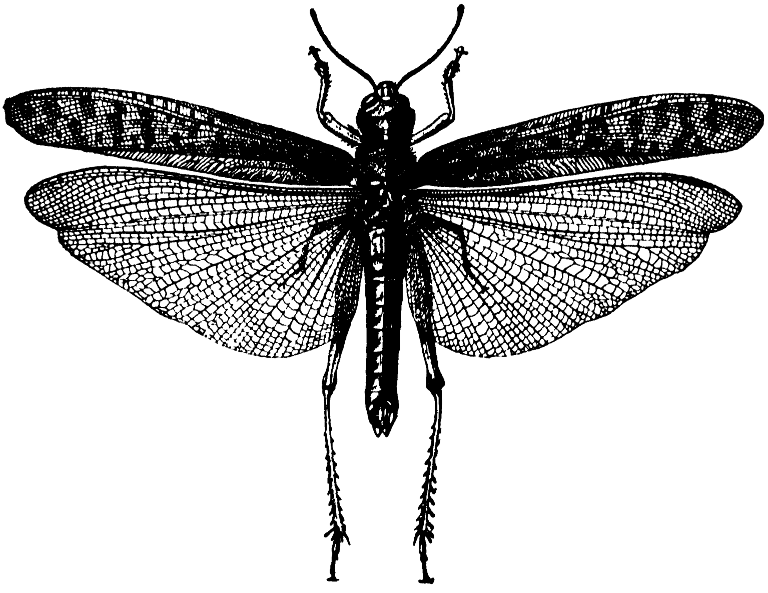

FIG. 252.—A TYPICAL MIGRATORY LOCUST, *SCHISTOCERCA GREGARIA*.

Reproduced by permission of the Trustees of the British Museum.

L. migratoria in its migratory phase is rare in western Europe but extends eastwards to the Philippines. In its solitary phase it ranges from Belgium to Japan and New Zealand: occasional stragglers have occurred in England while it is common in S. Europe. *Locusta* (*Locustina*) *pardalina* is peculiar to S. Africa, but its biology has been less fully studied. For a discussion on the phases of locusts, see p. 250.

The Acridiinæ are easily recognizable on account of the presence of a distinct spine on the prosternum between the anterior legs. Besides including most of the larger short-horned grasshoppers, almost all the destructive migratory grasshoppers or locusts are comprised in this sub-family, but they only constitute a small proportion of its species. Locusts are well known to migrate in vast swarms; one which passed over the Red Sea in 1889 was estimated to be 2,000 square miles in extent. During infestations in Cyprus official reports state that in 1881 1,300 tons of the eggs of locusts were collected and destroyed in that island. When an extensive swarm alights over a territory its members frequently convert, in a few hours, what were green and prosperous areas into desolate tracts of bare stems. One of the best known species is *Schistocerca gregaria* (Fig. 252) which causes great damage in northern Africa and extends into Persia, Afghanistan and northern India. It is probably to be identified with the locust of the plagues of Egypt quoted in the Book of Exodus. In 1869 it reached England in considerable numbers but has not occurred since. The Bombay locust (*Cyrtacanthacris succincta*) is apparently confined to India where it is occasionally a major pest (*vide* Lefroy, *Mem. Agric. Dept. India, Ent.* 1). A number of species of locusts occur in N. America, the widest spread being *Melanoplus femur-rubrum*: among others the Rocky Mountain locust *M. spretus* and the large *Schistocerca americana* may be mentioned. In the Prairie Provinces of Western Canada there have been locust infestations at intervals of about fifteen years which usually last two or more seasons. Of late years the two most destructive species have been *Melanoplus atlanis* and *Camnula pellucida*, the latter insect being a member of the Œdipodinæ.

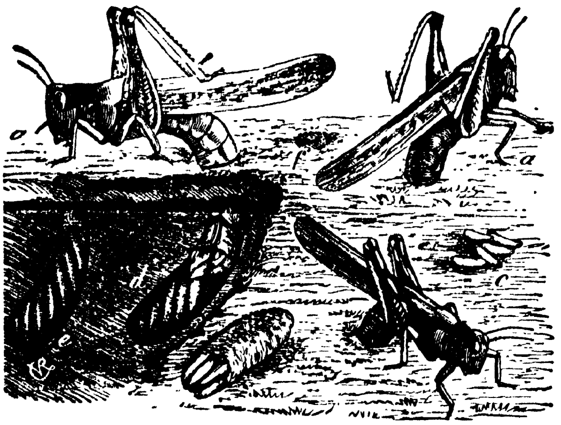

FIG. 253.—LOCUSTS IN THE ACT OF OVIPOSITION. *After* Riley.

FAM. TETTIGONIIDÆ (**Locustidæ**: Long-horned Grasshoppers).—The old name of Locustidæ, under which this family has been long known, is inapplicable because the genus *Locusta* L. belongs to the Acridiidæ. The Tettigoniidæ, therefore, are held to include, not locusts, but those insects commonly termed Katydids, green or long-horned grasshoppers, cave and camel crickets, etc. The antennæ are filiform, 30- or more jointed, and often extend, when reflexed, far beyond the apex of the abdomen. The tegmina slope obliquely downwards, and are usually membranous and of delicate structure. When closed, the left one usually overlaps the right, and they are generally slightly shorter than the wings (Fig. 254). Apterous forms, however, are common and include some of the largest of the species. The stridulating organ in the male is found at the base of the overlapping anal area of the left tegmen. It generally consists of a more or less rounded zone, bounded by a strongly curved vein, and crossed by a second vein which is thickened and bears a row of denticles. On the right tegmen there is a smooth transparent area of tense membrane, which is rasped by the denticles just referred to, and acts as a resonator when the tegmina

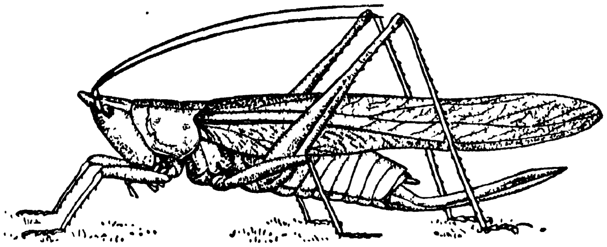

FIG. 254.—A LONG-HORNED GRASSHOPPER *NEOCONOCEPHALUS PALUSTRIS*. *After* Blatchley.

are in motion. The bright green Katydids (Phaneropterinæ) are the most notorious stridulators, their loud nocturnal notes sometimes resembling the syllables " Katy did, she did." In some groups wings are absent and the tegmina are reduced to the sound-producing portions only : this is seen, for example, in the Ephippigerinæ and Callimeninæ where, it may be added, the females also stridulate. A pair of auditory organs are situated on each fore-tibia near the proximal extremity of the latter (Fig. 96). Winged Tettigoniidæ are predominantly green and live amidst herbage, particularly bushes and trees. The wingless forms occur in caves or hollow trees, or beneath stones and logs, and are chiefly grey or brown in colour. Some of the apterous forms, however, are agile climbers and reach the tree-tops. The eggs of Tettigoniidæ are not enclosed in oothecæ, and the ovipositor frequently attains a great length, even exceeding that of the body (Fig. 45). In some cases it is used for depositing the eggs in the earth, but usually they are laid in plant-tissues of various kinds, often in neat longitudinal rows. Five or six ecdyses are prevalent and the members of this family are less predominantly herbivorous than the Acridiidæ : some forms (Saginæ) are notably carnivorous while others appear to be omnivorous.

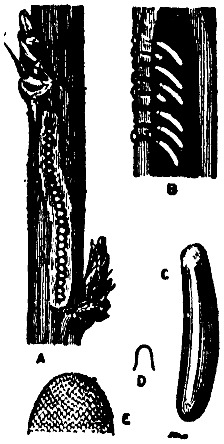

FIG. 255. — ŒCANTHUS NIGRICORNIS. A, egg punctures in stem of raspberry. B, longitudinal section. C, egg, magnified. D, projection of egg-cap. E, egg cap.

After Fulton, *N.Y. Agric. Exp. Sta. Tech. Bull.* 42.

The Tettigoniidæ are divided into fifteen sub-families and five, including nine species, extend into the British Isles. The largest of the latter species is *Phasgonura* (*Locusta*) *viridissima* which occurs in the southern half of England where it attracts attention from its strident notes. *Pholidoptera griseoaptera* has vestigial wings, and its range in England is very similar to that of the former insect.

FAM. GRYLLIDÆ (Crickets).—This family is directly related to the preceding one, and its members similarly possess long filiform antennæ, and usually an exserted ovipositor : they likewise stridulate by means of the friction of the tegmina and possess tibial auditory organs (Fig. 96). On the other hand, they resemble the Acridiidæ in having 3-jointed tarsi. The tegmina are folded flat over the abdomen but are bent abruptly downwards along the sides and, contrary to the usual rule among Orthoptera, the right tegmen usually overlies the left. The stridulating apparatus, as seen in *Gryllus*, occupies a larger area of the tegmina than in the Tettigoniidæ : each tegmen bears a file and a hardened area, or scraper, against which the file of the other tegmen works. There is also a vibratory area or tympanum on both tegmina. During stridulation the tegmina are elevated to an angle of about forty-five degrees with the abdomen and are moved backwards and forwards laterally, so as to produce friction between the files and scrapers. This movement throws the tympana in vibration so as to cause an audible sound. The sound-producing powers of the Gryllidæ are well exemplified in the house cricket : *Brachytrypes megacephalus* is stated to make a noise so penetrating that it can be heard at the distance of a mile. The auditory organs differ from those of the Tettigoniidæ in that those of the pair on each fore-leg differ from one another, the outer organ being larger than the inner one. Many crickets are entirely devoid of tegmina and wings : in *Trigonidium* the tegmina are arched and horny, and impart to these insects the appearance of Coleoptera. The ovipositor is slender and cylindrical, being more or less acicular, there is a pair of exceptionally long unjointed cerci and generally short anal styli.

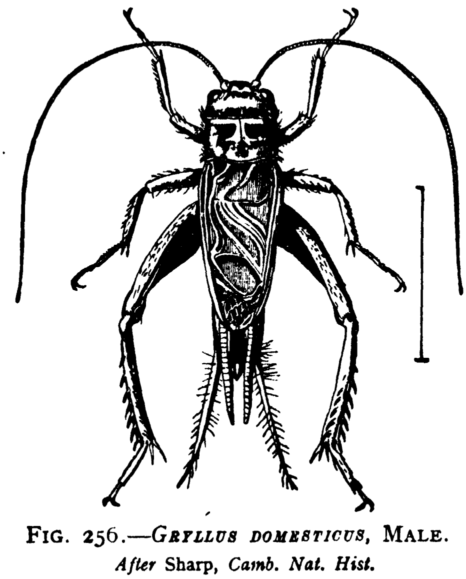

FIG. 256.—GRYLLUS DOMESTICUS, MALE.

After Sharp, *Camb. Nat. Hist.*

The eggs of most species are laid singly in the ground: a few of the subterranean forms deposit them in masses in underground chambers, while some Œcanthinæ place them in a single uniform row in the pith of twigs (Fig. 255). There are five ecdyses in the latter sub-family but among other Gryllidæ the number is stated to be higher. Crickets are, for the most part, omnivorous and frequent hot dry places, or live in holes or burrows, under logs among dead leaves, etc., while the Œcanthinæ occur on trees and bushes. Out of the seven sub-families into which Gryllidæ are divided only two occur in Britain. The Gryllinæ include the typical crickets of which there are three British species, viz. the ground cricket *Nemobius sylvestris*, the field cricket *Gryllus campestris* and the house cricket *G. domesticus* (Fig. 256). The Gryllotalpinæ comprise the mole crickets which are atypical in many respects: they are subterranean in habit and seldom seen. The fore-legs are greatly inflated and highly modified for fossorial purposes, the compound eyes are much reduced and there is no visible ovipositor. *Gryllotalpa gryllotalpa* L. (*vulgaris* Latr.) is the only European species and is rarely met with in Britain (Fig. 257). The Myrmecophilinæ (*vide* Schimmer, 1909) are very small subspherical apterous crickets that live in association with ants and occur in Europe, Asia and America (Fig. 258). *Mogoplistus* and its allies are covered with minute scales and are often regarded as a separate sub-family. The Œcanthinæ (*vide* Fulton, 1915) are a large group of pale-coloured tree crickets and the Tridactylinæ include the sand or pygmy mole crickets. In the latter insects the tegmina bear no stridulatory organs, auditory organs are likewise wanting and the fore and middle tarsi are 2-jointed and the hind pair 1-jointed or wanting. The only European species, *Tridactylus variegatus*, is widely distributed and extends into Asia. The Eneopterinæ include the larger brown bush crickets mostly found in the Old World.

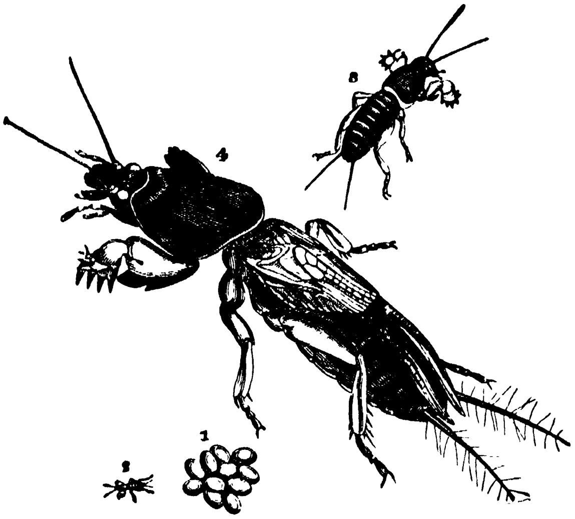

FIG. 257.—*GRYLLOTALPA GRYLLOTALPA*, WITH EGGS AND NYMPHS.

After Curtis.

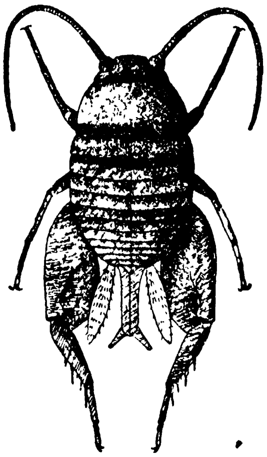

FIG. 258.—*MYRMECOPHILA ACERVORUM*, FEMALE, × 5.

After Chopard, "Faune de France."

Supplement on the Biology and Phases of Locusts

Locusts are species of short-horned grasshoppers which at times become predominantly gregarious and migrate considerable distances in large swarms. In 1921 Uvarov advanced the theory that each species of true locust is polymorphic or, in other words, it does not remain consistent in all its characters—i.e. it develops into forms or *phases* differing from one another structurally and biologically. According to the phase theory each species exists in a migratory phase (*phasis gregaria*) and a solitary phase (*phasis solitaria*), hitherto named by taxonomists as separate species. These two phases are extreme forms and are connected by intermediates of different grades forming the *phasis transiens.*

The *phasis gregaria* or swarming phase is characterized, in its nymphal instars, by the great predominance of black and yellow or orange coloration which develops irrespective of the nature of the environment. The adults have the pronotum usually somewhat concave, prominently constricted and with no dorsal carina. Biometrical studies show differences in size and proportions of certain organs, as compared with *phasis solitaria*, the most conspicuous being the proportionately greater length of the wings. On reaching sexual maturity colour changes occur, especially in the males. This phase is definitely gregarious, both as nymphs and adults.

The *phasis solitaria* is characterized by the nymphs being extremely plastic in their coloration and showing a strong tendency to simulate that of their immediate surroundings. The imagines may have the pronotum arched owing to a longitudinal carina, and there is no constriction. They exhibit no marked sexual changes of colour and behave as ordinary solitary grasshoppers or, in other words, betray no gregarious instincts.

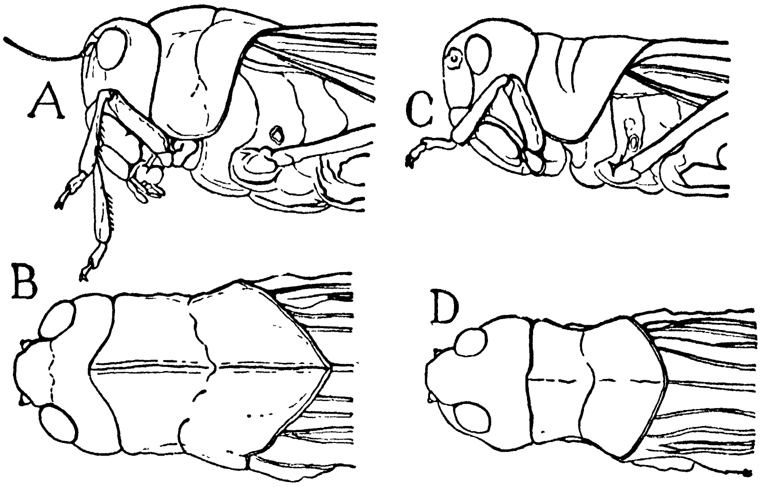

FIG. 259.—FORM OF THORAX IN PHASES OF THE LOCUST, *LOCUSTA MIGRATORIA MIGRATORIOIDES*.

A, B, phasis solitaria ; C, D, phasis gregaria. *After* Faure.

The *phasis transiens* shows a tendency towards one or other of the preceding phases according to whether it is developing towards the solitary or gregarious condition.

The phase theory has recently been subjected to experiment and, given suitable temperature, humidity and food, it has been found possible to induce either phase to develop from the other. In a few words, individuals reared from the egg in isolation develop evident solitaria characters while those reared collectively in large numbers develop into the phase gregaria (Faure, 1932, 1933 ; Ballard and others, 1932). Field observations by Johnston (1926) also lend support to the phase theory.

Faure (1932) believes that the differences between the two phases are mainly the result of the intense activity that is betrayed by locusts when the nymphal stages are developing under gregarious conditions. The enormous amount of muscular activity tends to bring about the constriction of the pronotum and the increased length of the wings. At the same time it is suggested that the increased metabolism results in the production of the characteristic black and yellow coloration.

The manifold environmental factors which result in phase production in the field are, as yet, not adequately explained but it is evident that the gregaria phase only develops in specific breeding areas, where a particular combination of ecological conditions prevail. When these conditions are favourable great masses of migratory individuals leave their breeding grounds in dense swarms. Their resulting progeny develop, as a rule, into solitaria, or transiens, individuals wherever their environment is of a character different from the original breeding grounds.

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Order 5. DERMAPTERA (Earwigs)

ELONGATE INSECTS WITH TYPICAL BITING MOUTH-PARTS: SUPERLINGUÆ DISTINCT: LIGULA 2-LOBED. FORE-WINGS MODIFIED INTO VERY SHORT LEATHERY TEGMINA DEVOID OF VEINS: HIND-WINGS SEMICIRCULAR, MEMBRANOUS, WITH THE VEINS HIGHLY MODIFIED AND DISPOSED RADIALLY. APTEROUS FORMS COMMON. TARSI 3-JOINTED. CERCI UNJOINTED AND ALMOST ALWAYS MODIFIED INTO HORNY FORCEPS: AN OVIPOSITOR USUALLY ABSENT. METAMORPHOSIS SLIGHT OR WANTING.

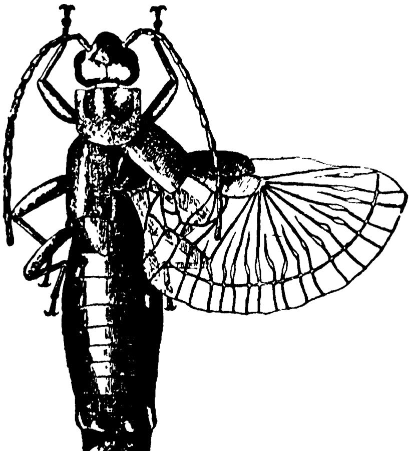

FIG. 260—*FORFICULA AURICULARIA*, MALE WITH RIGHT WING EXTENDED.
After Chopard, " Faune de France."

The general form and appearance of these insects are well exemplified in the common " earwig," *Forficula auricularia* (Fig. 260) which is abundant throughout Europe: it also occurs in other parts of the Palæarctic region and has been introduced into N. America. About 900 species of the order are known and, for the most part, they exhibit no very marked variations in form or structure. In habits they are mostly nocturnal and many tropical species are attracted to a light. During the day they hide away in the soil, under bark and stones, or among herbage, etc. Excepting *Labia minor*, the European species rarely take to the wing and, notwithstanding the well-developed wings of the common earwig, the latter insect has only on very rare occasions been noted to use them. The majority of species are probably omnivorous but more especially incline to animal food. In captivity *Labidura riparia* will readily devour flies and other insects in preference to vegetable food. *Forficula auricularia* is frequently destructive to flower petals and tender foliage: it is, however, an unsettled point whether it is normally carnivorous, but the species is known to devour both living and dead insects (Brindley, *Proc. Camb. Phil. Soc.* 1918). The term "earwig" possibly took its origin from the fact that these insects have been known to use the human ear for purposes of concealment: on the other hand it has been suggested that the word is a corruption of " ear-wing " in allusion to the form of the hind-wings. The function of their most characteristic organs—the forceps—is wrapped in a certain amount of obscurity. They have been reputed to use these appendages for opening and folding up the wings: on several occasions they have been known to impale their prey with them, but in all probability they are principally brought into use as organs of offence and defence. When alarmed, or molested, the extremity of the abdomen is often upraised and the forceps widely opened in a threatening manner. The most interesting feature in the biology of earwigs is the parental care that is exercised for the eggs and young. This trait was first observed by De Geer in 1758 and others after him have recorded the same facts. The eggs are deposited in the soil in a group, and the female rests over them very much like a hen and her chickens. The newly hatched young also remain around and beneath their parent, who exhibits evident care for them until they are able to look after themselves. If the eggs be removed, and distributed among soil contained in a box, De Geer states that in a few days they are all collected together again and the female seated over them.

External Anatomy.—Among the more noteworthy structural features is the broad horizontal *head*, frequently with a distinct Y-shaped epicranial suture. The antennæ consist of from 10 to about 50 joints, the eyes are circular and there are no ocelli. In *Arixenia* the eyes are vestigial, and they are atrophied in *Hemimerus*. The mandibles are broad and strong and almost always carry two apical teeth. The maxillæ closely resemble those of the Orthoptera while the labium differs in the ligula, which consists of a single pair of lobes (Fig. 12). The homologies of the latter are uncertain but, in view of the tendency to atrophy exhibited by the glossæ in the Acriddiiæ, it is possible.that these parts have totally disappeared in the Dermaptera, and the lobes that remain would therefore be interpreted as the paraglossæ. The hypopharynx is well developed, and the superlinguæ are represented by a pair of relatively large lobes recalling those of the Thysanura Entognatha. The *cervicum* is supported by tergal, pleural, and sternal sclerites. According to Snodgrass the *thorax* presents features which approximate more closely to those found in Coleoptera than in Orthoptera. The pronotum is a large and more or less quadrangular shield: a postnotum is wanting from the mesonotum, but is present in the metanotum although fused with the first abdominal tergum. Tegmina and wings are absent in *Anisolabis*, the Brachylabini and in *Arixenia* and *Hemimerus*, while the wings vary greatly in development in other members of the order. The tegmina are short, truncated structures devoid of veins, and meet along the median line, thus resembling the elytra of the Staphylinidæ. The large semicircular wings are almost entirely composed of the greatly extended anal area: the pre-anal portion of the wing is chitinized and contains two reduced longitudinal veins (R and Cu). The greater part of the wing is supported by a series of secondarily developed radially disposed branches. The wings are folded longitudinally in a fan-like manner, accompanied by two folds in a transverse direction and, in this way, they are stowed beneath the small tegmina. The legs do not call for special mention, and the tarsi are 3-jointed in all cases.

The *abdomen* is 11-segmented; the 1st tergum is fused with the metathorax and the 11th is represented by the small pygidium. In the females of the Forficulidæ and Hemimeridæ the 8th and 9th terga are greatly reduced and invisible without dissection. In the *Arixenidæ*, on the other hand, the nymphal or ancestral condition is maintained in that both sexes have the full complement of terga, with only very slight reduction of the 8th and 9th shields in the female. The 1st sternum is always wanting, while sterna 2 to 9 in the male and 2 to 7 in the female are clearly visible. The 9th sternum in the male largely overlies the 10th, the latter being represented in both sexes by a pair of plates at the base of the cerci. In the female the 7th sternum completely conceals the 8th and 9th (Fig. 261). According to Berlese a vestigial 11th sternum is present in both sexes and takes the form of a minute divided plate close to the anus. In all the Forficulidæ the cerci are modified into unjointed forceps. The latter present great diversity of form among different species, and are often variable within the limits of a single species as in *Forficula auricularia* (Bateson & Brindley, *Proc. Zool. Soc.* 1892). In the females of almost all earwigs they are shorter than in the males, being as a rule straight and unarmed. In *Hemimerus* the cerci are represented by hairy unjointed styliform appendages. The cerci of *Arixenia* resemble those of *Hemimerus*, except that they are bowed inwards in the male, and bear a closer resemblance to the forceps of true earwigs.

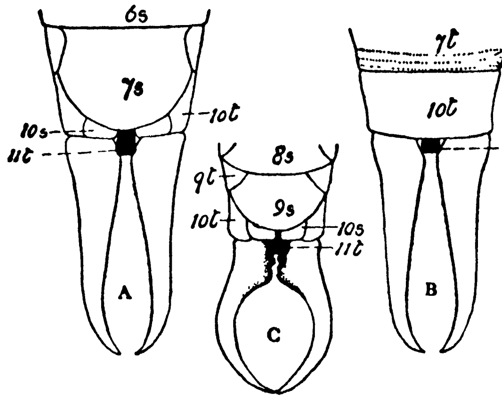

FIG. 261.—*FORFICULA*, TERMINAL ABDOMINAL SEGMENTS.

A, female (ventral). B, female (dorsal). C, male (ventral). *s*, sterna; *t*, terga.

Internal Anatomy.—The *alimentary canal* (Fig. 262) is of a very uniform structure throughout the order. The œsophagus leads into the crop which is followed by a small globular gizzard. The mid-intestine has no enteric cœca and is slightly coiled posteriorly, but in *Arixenia* it forms nearly two complete coils. The Malpighian tubes vary from eight or ten to about twenty, and are grouped in bundles. In *Forficula* Bordas states there are eight or ten tubes grouped in two bundles, while Jordan mentions four bundles containing 5, 3, 4, 4 tubes respectively. The hind-intestine presents a partial or, in *Arixenia*, a complete convolution, and there are six rectal papillæ. The *nervous system* (Fig. 58) appears to be very constant and, in addition to the two cephalic centres, there are three thoracic and six abdominal ganglia. The *tracheal system* communicates with the exterior by means of ten pairs of spiracles as in Orthoptera. The *female reproductive organs* (Fig. 163) are divisible into two types. In *Forficula* there are three rows of numerous, very short, polytrophic ovarioles, distributed at regular intervals along the greater part of the length of each oviduct. In *Labidura riparia*, *Arixenia* and *Hemimerus* the ovarioles are much fewer, and are disposed in a single series. In *Labidura* there are five elongate ovarioles: in *Hemimerus* there are eight (Jordan) or 10–12 (Heymons) while in *Arixenia* there are fewer (Jordan). In the two last mentioned genera the ovarioles are very short, each containing a single egg, and viviparous reproduction occurs. According to Heymons (1912) a maternal placenta is present in *Hemimerus* and envelops the embryo. At the anterior extremit[illegible]e latter the placenta forms a large cell-mass and, lying beneath [illegible] fœtal

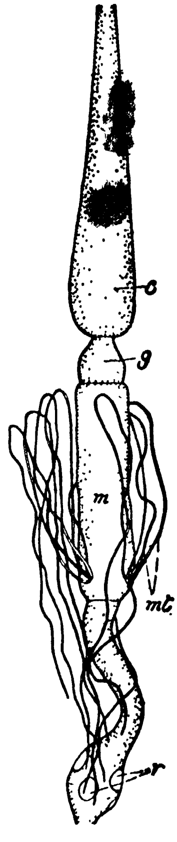

FIG. 262.—*FORFICULA*, ALIMENTARY CANAL.

c, crop; *g*, gizzard; *m*, mid-intestine; *mt*, Malpighian tubes; *r*, rectal [illegible]pillæ.

placenta which is developed as a proliferation of the amnion and serosa in that region. The whole placental organ, thus formed, is in direct connection with the body of the embryo by means of a diverticulum of the head-cavity, known as the cephalic vesicle. The embryos, to the number of about six at a time, are nourished *in situ* within their respective ovarioles, until they develop into young insects and ready for birth. The *male reproductive organs* (Fig. 159) exhibit considerable differences among various genera. In *Forficula* and *Anisolabis* the testes each consist of a pair of elongate closely apposed follicles: in *Hemimerus* the follicles are likewise paired, but are filiform and tightly coiled: in *Arixenia* the testes are compact and globular, each consisting of sixteen short follicles. The vasa deferentia are very slender, and in *Anisolabis* and *Hemimerus* they dilate posteriorly to form vesiculæ seminales: the latter open, in *Hemimerus*, into a small vesicle which communicates with the base of the penis. The ejaculatory duct is stated to be wholly mesodermal in origin and, in *Labidura*, Meinert has shown that this canal is paired. It opens externally by double apertures and ædeagi, whereas in other members of the order one ejaculatory duct atrophies, although a rudiment of it may apparently persist in a few cases.

Life-History and Post-embryonic Growth.—The eggs of Dermaptera are pale coloured, being whitish in *Forficula*, and elliptical with smooth surfaces. *F. auricularia* in Europe lays, according to Brindley, an average of 23 eggs: in America Jones (*Bull.* 566 *U.S. Dept. Agric.*) places the number as high as 50–90. The eggs have been found during winter or early spring, and in England Chapman mentions that six ecdyses are passed through, while in America Jones records four. The adult condition is assumed during the summer, and there appears to be a single generation in the year. The young nymphs resemble their parents in general form, except that the forceps are simple and more or less styliform (Fig. 263). In *Diplatys*, the forceps are preceded by jointed cerci in the nymphal stages. According to Green, in *D. gerstæckeri* nymphs 2·5 mm. long bear 14-jointed cerci which are equal in length to the body. During subsequent instars the number of joints increases up to 45, and the cerci attain a length nearly double that of the body. In the pre-imaginal instar they become abruptly curtailed to a single joint, within which the future forceps can be made out. In almost all other earwigs the forceps are not preceded by cerci, and no trace of jointing in these organs has been detected in the few embryos that have been examined.

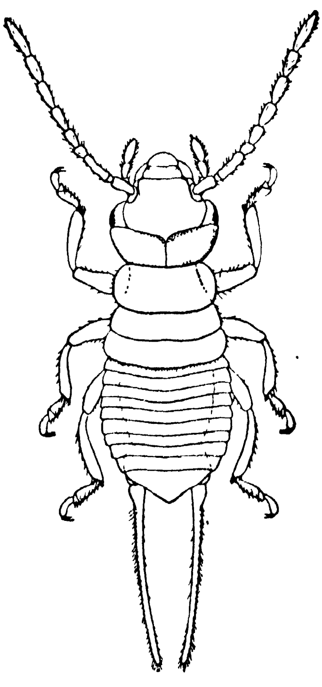

FIG. 263.—*FORFICULA*, NEWLY-HATCHED NYMPH, × 15.

Classification.—The Dermaptera have been monographed by Burr (1911) and general information on the order is given in the earlier work (1910) of that authority. There are eight families as follows.

Sub-order I. FORFICULINA (Earwigs)

FREE-LIVING FORMS. EYES WELL DEVELOPED: WINGS OFTEN PRESENT: CERCI MODIFIED INTO HORNY FORCEPS.

Superfam. I. **Labiduroidea.**—Body normally convex: ædeagus paired: forceps not sickle-shaped: 11th tergum and telson present as separate plates.

FAM. PYGIDICRANIDÆ.—Femora compressed and usually keeled. *Pygidicrania, Diplatys.*

* **FAM. LABIDURIDÆ.**—Femora not compressed or keeled. *Anisolabis, Labidura.*

Superfam. II. **Apachyoidea.**—Body usually much flattened: ædeagus paired: forceps sickle-shaped: 11th tergum and telson fused together with 10th segment.

FAM. APACHYIDÆ.—*Apachyus.*

Superfam. III. **Forficuloidea.**—Ædeagus unpaired: 10th tergum (pygidium) well developed: 11th tergum and telson vestigial or absent.

* **FAM. FORFICULIDÆ.**—Second tarsal segment bilobed. *Forficula, Apterygida.*

FAM. CHELISOCHIDÆ.—Second tarsal segment produced into a narrow lobe beneath third segment. *Chelisoches.*

* **FAM. LABIIDÆ.**—Second tarsal segment unmodified. *Labia, Prolabia, Spongiphora.*

Families marked * occur in Britain.

Sub-order II. ARIXENINA

ECTOPARASITIC. EYES VESTIGIAL. APTEROUS: CERCI NOT HORNY BUT ARCHED AND HAIRY.

FAM. ARIXENIIDÆ.—This small group is constituted by the genus *Arixenia* with two species, viz. *A. esau* Jord. from Sarawak and *A. jacobsoni* Burr from Java (Fig. 264). The first mentioned species was found in the breast-pouch of the bat *Cheiromeles torquatus*: the second species has been met with in large numbers on

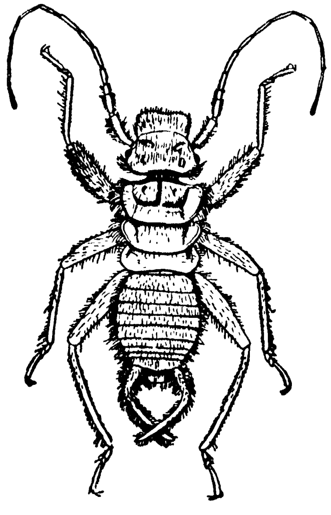

FIG. 264.—*ARIXENIA JACOBSONI*, MALE.
After Burr, *Ent. Month. Mag.*, 1912.

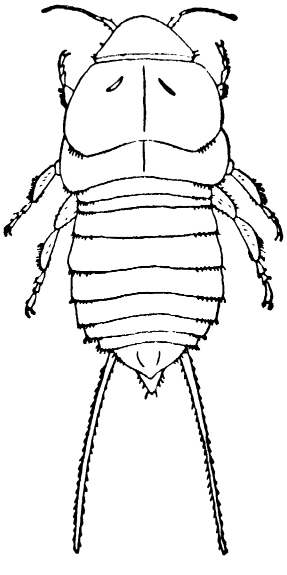

FIG. 265.—*HEMIMERUS TALPOIDES.*
Adapted from Hansen.

guano in a cave much resorted to by bats. *Arixenia* is apterous and viviparous, the eyes are greatly reduced, and the mandibles are strongly flattened with their inner edges rounded and clothed with bristles. The cerci are feebly chitinized and hairy: they are unjointed and somewhat bowed, which gives them the appearance of incipient forceps. For further information on the genus vide Jordan (1909A), Burr and Jordan (1913).

Sub-order III. HEMIMERINA

ECTOPARASITIC. EYES ABSENT: APTEROUS: CERCI LONG, STRAIGHT AND UNSEGMENTED.

FAM. HEMIMERIDÆ.—This family is composed of the single genus *Hemimerus* of which *H. talpoides* Walk. (Fig. 265) lives as an ectoparasite of the rat *Cricetomys gambianus* in Sierra Leone, and is believed to feed upon the epidermal products of its host. *H. hanseni* Shp. from Cameroons and Uganda is often regarded as constituting a second species. *Hemimerus* is apterous and viviparous, devoid of eyes, and the cerci are feebly chitinized, unjointed, hairy appendages which resemble those of the Gryllidæ. The structure of this remarkable insect has been investigated by Hansen (1894), Jordan (1909) and Heymons (1912): it is an annectant form connecting the Dermaptera with the Orthoptera.

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Order 6. PLECOPTERA (Perlaria : Stone Flies)

SOFT-BODIED INSECTS OF MODERATE TO RATHER LARGE SIZE WITH ELONGATE, SETACEOUS ANTENNÆ. MOUTH-PARTS WEAK, OF THE BITING TYPE : MANDIBLES NORMAL OR VESTIGIAL, LIGULA 4-LOBED. WINGS MEMBRANOUS, HELD FLAT OVER THE BACK IN REPOSE, HIND PAIR USUALLY THE LARGER, WITH WELL-DEVELOPED ANAL LOBES. VENATION VARIABLE, OFTEN CONSIDERABLY SPECIALIZED: VEIN M 2-BRANCHED. TARSI 3-JOINTED. ABDOMEN USUALLY TERMINATED BY LONG MULTI-ARTICULATE CERCI : OVIPOSITOR WANTING. METAMORPHOSIS HEMIMETABOLOUS : NYMPHS AQUATIC, CAMPODEIFORM, WITH THE ANTENNAE AND USUALLY THE CERCI ELONGATE : TUFTED TRACHEAL GILLS, WHICH ARE VARIABLE IN POSITION, COMMONLY PRESENT.

The Plecoptera are a small order, whose members are of considerable interest on account of the many archaic features in their structure, and the aquatic habits of their nymphs. The imagines have the same general characters as those of the Orthoptera, but the mouth-parts are weaker, there is never more than a slight difference in texture between the fore- and hind- wings, and the coxæ are small. They are poor fliers, and do not wander far from water. Their habitation is the margins of streams and lakes, particularly in hilly districts : they are commonly found resting upon stones, tree-trunks or palings near the water's edge, while the green forms frequent herbage. The larger species are well known to anglers as a bait for trout. The nymphs are exclusively aquatic, living beneath stones in clear water, particularly in streams with stony beds, and places where there are waterfalls, or where the water is otherwise well aërated. They do not live in stagnant pools or polluted streams. Very little is known concerning the feeding habits of the imagines and, in certain cases, they apparently do not feed at all.

About thirty species of the order have been recognized in the British Isles, but no general work dealing with these forms is available. Among various scattered notes and descriptions, relating to British species, the most important are those of Morton (*Trans. Ent. Soc.* 1894, 1896 : *Ent. Month. Mag.* 38, 43, 65) : the work of Klapálek (1909) is also useful.

External Anatomy.—The antennæ are long and setaceous, with a large number of small joints. Compound eyes are well developed, and there are three (more rarely two) ocelli. The mouth-parts (Fig. 266), although completely formed, are usually weak structures: the mandibles are normally developed in the greater number of species, but in the Pteronarcidæ and Perlidæ they are in the form of vestigial flexible lamellæ. The maxillæ consist of the typical sclerites and their palpi are 5-jointed. In the labium, the mentum is large, the prementum is sometimes divided, and both glossæ and paraglossæ are evident : the labial palpi are 3-jointed. The whole of the after-body is somewhat flattened, none of the parts are strongly chitinized, and much shrivelling takes place in dried specimens. The thorax has been studied more particularly in *Capnia* and *Leuctra*, and exhibits a very primitive condition of its sclerites. The prothorax is large and mobile, while the meso- and meta-thorax are subequal segments, exhibiting the primary four-fold division into tergites. The thoracic sterna have the full complement of sternites, excepting that the post-sternellum is absent from the metathorax. An additional sclerite of uncertain homology is present between the sternellum and post-sternellum in *Capnia*: by some authorities it is regarded as indicating a five-fold primary division of the thoracic sternum. Newport (1851) described in *Pteronarcys* a pair of openings between the legs on each of the thoracic sterna, these apertures being the mouths of the invaginations forming the furcæ of those segments. The wings are membranous: the hind-wings are almost always considerably larger than the anterior pair, and a coupling-apparatus is not developed. The anal lobe is folded fanwise against the body when in repose. The tracheation in the nymphs has been studied in several genera:—it closely resembles the hypothetical type in the absence of the transverse basal trachea (Fig. 268). The fully developed wings exhibit great instability of the subordinate veins, and individuals are frequently unlike with respect to the wing venation of the two sides of the body. In some species, *Perla maxima* for example, both macropterous and micropterous males occur, the latter forms being prevalent in the more northern latitudes. *Nemoura glacialis*, *Isogenus nubecula*, and other species similarly exhibit this phenomenon, the wings in the males often being so short as to be useless for flight. The most archaic type of venation is found in the Eustheniidæ (Fig. 269): in this family the archedictyon is present over all parts of the wings, Rs exhibits three or more branches, and there is a large fan-like anal lobe to the hind-wings carrying a number of anal veins. Various transitional genera (Fig. 270) lead to more specialized types such as *Capnopsis*. In the latter genus the archedictyon has disappeared, Rs is 2-branched in the fore-wing, and unbranched in the hind-wing, while the latter has lost the anal lobe and vein 1 A.

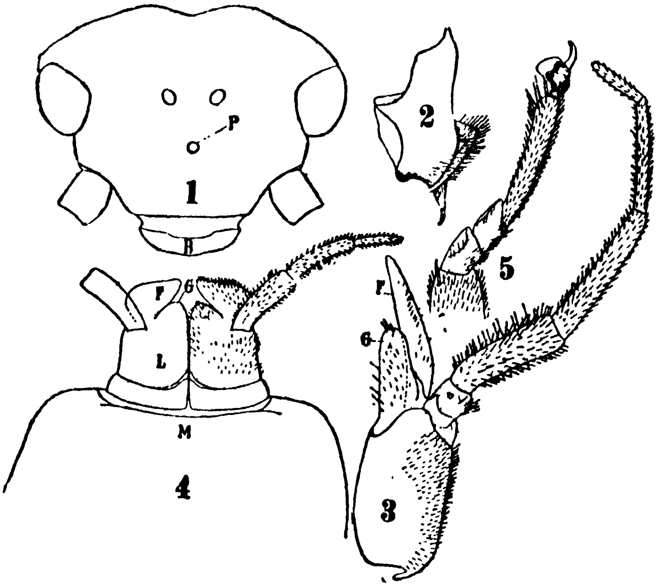

FIG. 266.—*PERLA MAXIMA.*

1, frontal view of head; P, ocelli, B, labrum. 2, mandible; 3, maxilla; F, galea, G, lacinia. 4, labium; F, paraglossa, G, glossa, L, prementum. 5, tarsus. *After* Silvestri.

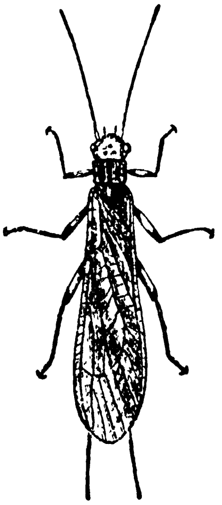

FIG. 267.—*PERLA MAXIMA*, natural size. *After* Pictet.

The abdomen is composed of ten evident segments, together with vestiges of an 11th segment. An ovipositor is absent in the female, and anal styli are likewise wanting in the male. Cerci are characteristic of the order, and are usually long multi-articulate appendages of a primitive type: in the Nemouridæ, however, they are small single-jointed structures.

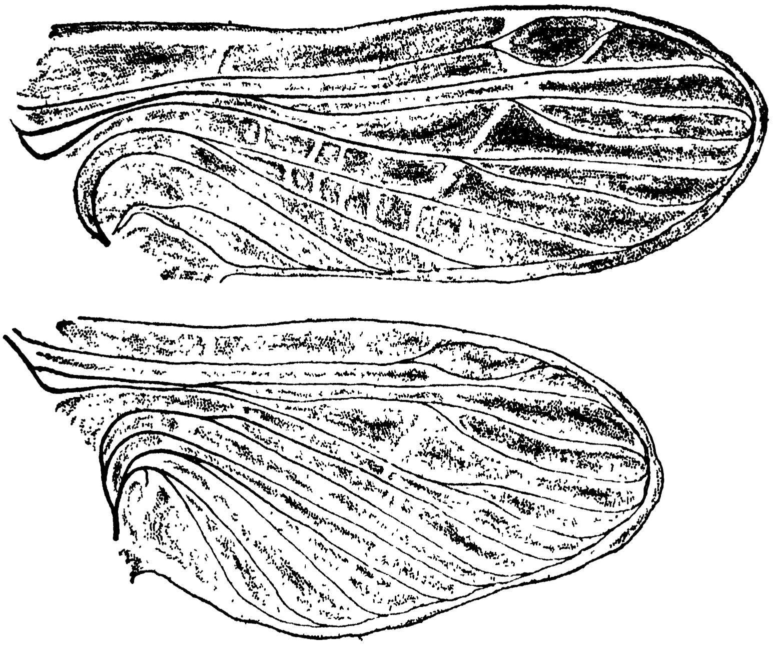

FIG. 268.—*Nemoura*, WINGS OF A NYMPH.

After Comstock and Needham.

Internal Anatomy.—The internal anatomy has been investigated by Pictet (1841–42), Newport (1851), Imhof (1881) Schœnemund (1912) and others. The œsophagus is exceedingly long and, in *Pteronarcys*, extends into the 4th abdominal segment: the gizzard is wanting or rudimentary, and the mid-gut is small. In *Perla* there are ten anterior enteric cœca, the lateral pair being the largest. The hind intestine is short and the Malpighian tubes vary between about twenty and sixty. A pair of salivary glands is present. Both the supra- and infra- œsophageal ganglia are small: in *Pteronarcys* there are three thoracic and eight abdominal ganglia, but in *Perla* certain of the latter have undergone coalescence, with the result that there are only six evident ganglia in the abdomen. The reproductive organs are peculiar in that the gonad

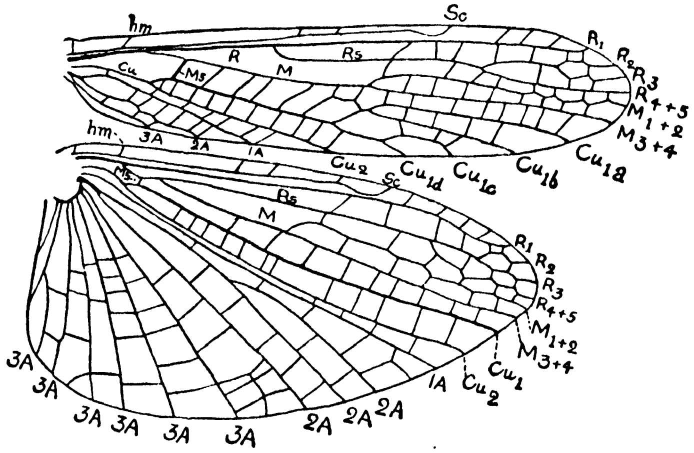

FIG. 269.—*Stenoperla prasina*, NEW ZEALAND, WINGS.

After Tillyard, 1923.

of either side is joined transversely with its fellow, the two forming an arch-like organ, consisting of a number of ovarioles, or ovoid testicular follicles, as the case may be. At the point of union of the sexual ducts there may be a pair of tubular vesiculæ seminales in the male, and a large sac-like spermatheca in the female. The tracheal system opens to the exterior by two pairs of thoracic and eight pairs of abdominal spiracles.

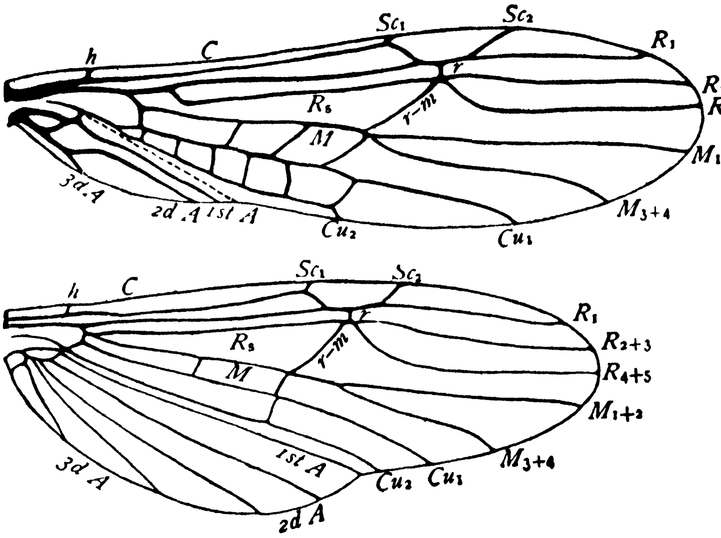

Fig. 270.—*Nemoura*, Wings.

After Comstock, " Wings of Insects."

Oviposition and Post-Embryonic Growth.—Plecoptera are notable on account of the very large number of eggs laid by a single individual, which, in some cases, attains 1,500 to 2,000. Few direct observations of the act of oviposition are available, but it appears in several species that the eggs are dropped on the surface of the water, and distributed by the current before they reach the bottom. Miall states that the eggs of *Perla* are black: they project from the abdomen, being loosely held together by a transparent skin, and are deposited in the water. According to McLachlan (*Ent. Month. Mag.* 1865) the females of *Leuctra* carry their eggs on their backs, extruding them from the upturned apex of the body and, at the same time, pushing them forwards towards the thorax.

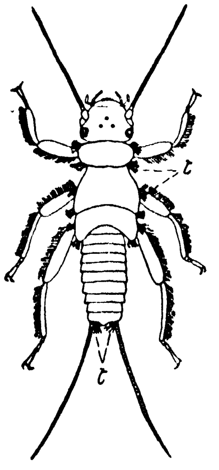

Fig. 271.—*Perla* sp., Nymph.

t, tracheal gills.

The nymphs (vide Pictet, 1841–42; Klápalek, 1909; Schœnemund, 1912) resemble the adults very closely in their general form but, unlike the Orthoptera, metamorphosis is of the hemimetabolous type. Apart from the absence of fully developed wings, the characters which differentiate the nymphs from the adults are adaptive in nature, fitting them for an exclusively aquatic existence. Plecopterous nymphs are characterized by their long multi-articulate antennæ, and their similarly elongate cerci (Fig. 271): in some cases (e.g. Nemouridæ), however, the latter appendages are in the form of minute single-jointed structures. The head may carry both ocelli and compound eyes: the legs are long, laterally fringed with natatory hairs, and terminated by paired claws. The tracheal system is apneustic, and respiration is either cutaneous or branchial. The nymphs are active swimmers, preying upon various small forms of aquatic life including Ephemerid nymphs, larval Chironomids, etc. The most primitive type of nymph is found in the Eustheniidæ: here there are five or six pairs of lateral abdominal appendages which function as gills (Tillyard). In other families the nymphs breathe by means of secondary tufts of tracheal gills. In *Perla bipunctata*, for example, six pairs of the latter are carried near the bases of the legs and at the junction of adjacent segments on the ventral aspect of the thorax; there is also a gill-tuft near the base of each cercus. The branchiæ, however, are very variable in position: in the Leptoperlidæ they are only developed around the anus and in species of *Nemoura*, for example, they assume the form of lamellate outgrowths on the prosternum. Plecoptera are also remarkable from the fact that the branchiæ may persist in a somewhat shrivelled, non-functional condition in the imagines. Thus, Newport showed many years ago that in the adult *Pteronarcys* branchiæ are present on each of the thoracic segments, and at the base of the abdomen: they are also evident in other genera although often very inconspicuous.

The time occupied in development appears to range from about a year in the smaller forms up to 3½ or 4 years in the larger species. According to Wu (1923) a species of *Nemoura* passed through 22 instars and the same number was observed by Samal (1923) in *Perla abdominalis*. In *P. cephalotes* Schœnemund (1912) recorded 33 ecdyses during a period of three years.

Classification.—The most primitive families occur in the southern hemisphere, the Eustheniidæ, for example, being confined to the Australian region and Chili, while only the more specialized families are found northwards into the holarctic region. Those marked * in the table below are represented in the British Isles. For a bibliography of the order *vide* Claasen (1931).

Key to the families of Plecoptera based upon the classification of Tillyard (1921, 1923).

1 (2).—Anal lobe of hind-wing with archedictyon, margin entire. *Eusthenia, Stenoperla.* EUSTHENIIDÆ
2 (1).—Anal lobe of hind-wing without archedictyon, margin incised at apex of Cu_2.
3 (4).—Anterior coxæ closely approximated: mandibles vestigial: archedictyon present except on anal lobe. *Pteronarcys.* PTERONARCIDÆ
4 (3).—Anterior coxæ widely separated.
5 (6).—Mandibles vestigial: clypeus and labrum hidden beneath a frontal shelf: 3rd tarsal joint longer than 1st + 2nd. *Perla, Chloroperla.* *PERLIDÆ
6 (5).—Mandibles, clypeus, and labrum normal: 3rd tarsal joint not longer than 1st + 2nd.
7 (8).—With more than six anal veins in hind-wing. *Austroperla, Tasmanoperla.* AUSTROPERLIDÆ
8 (7).—With six or fewer anal veins in hind-wing.
9 (10).—No true anastomosis joining main veins from R to Cu_1 near middle of wings: distal cross veins present. *Leptoperla, Gripopteryx.* LEPTOPERLIDÆ
10 (9).—A true anastomosis joining main veins from R to Cu_1 near middle of wings: distal cross veins usually absent.
11 (12).—Cerci 1-jointed, vestigial. *Tæniopteryx, Nemoura, Leuctra.* *NEMOURIDÆ
12 (11).—Cerci long, multi-articulate. *Capnia.* *CAPNIIDÆ

Literature on Plecoptera

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Order 7. ISOPTERA (Termites or white ants)

SOCIAL AND POLYMORPHIC SPECIES LIVING IN LARGE COMMUNITIES COMPOSED OF WINGED AND APTEROUS REPRODUCTIVE FORMS TOGETHER WITH NUMEROUS APTEROUS, STERILE, SOLDIERS AND WORKERS. MOUTH-PARTS OF THE TYPICAL BITING TYPE : LIGULA 4-LOBED. WINGS VERY SIMILAR, ELONGATE AND MEMBRANOUS, SUPERPOSED FLAT OVER THE BACK WHEN AT REST AND CAPABLE OF BEING SHED BY MEANS OF BASAL FRACTURES : ANTERIOR VEINS STRONGLY SCLEROTIZED, REGULAR CROSS-VEINS WANTING AND AN ARCHEDICTYON OFTEN PRESENT. TARSI ALMOST ALWAYS 4-JOINTED. CERCI SHORT OR VERY SHORT : GENITALIA WANTING OR RUDIMENTARY IN BOTH SEXES. METAMORPHOSIS SLIGHT OR ABSENT.

The Isoptera are usually known as termites or " white ants " ; the latter expression, however, is unfortunate since these insects are very distantly related to the true ants or Formicoidea. Their invariable habit of living in densely populated societies, along with their pale coloration, has given rise to the popular expression of " white ants," but the use of the word termites is preferable to the latter, being convenient and not open to objection. Different as the termites are from the true ants, the two groups offer certain striking analogies of habits and structure. Their remarkable social life and the presence of specialized wingless individuals, known as soldiers and workers, are cases in point.

Termites abound throughout the tropics of the world and also occur in most warm temperate countries. Fully 1,500 species have been described and, of these, the vast majority occur south of the holarctic region. Only two species, *Calotermes flavicollis* and *Leucotermes lucifugus*, are common in Europe, but these do not extend their range into the British Isles.

A termite community includes several castes or types of individuals which live in habitations, or termitaria, of extremely varied kinds. The castes are five in number, and are divisible into reproductive and sterile forms consisting of individuals of both sexes. The reproductive castes comprise (*a*) completely chitinized macropterous or fully-winged forms whose mission in life is the formation of new colonies (Fig. 272) : (*b*) slightly chitinized brachypterous forms : and (*c*) slightly chitinized apterous forms (Fig. 285). In addition to the foregoing, a termite colony usually contains a royal pair—the queen and king : these are commonly deälated individuals of the fully-winged caste and are the original founders of the colony (Fig. 284). The sterile castes consist of (*a*) soldiers and (*b*) workers which are apterous males and females adapted for special non-reproductive functions. Every colony also contains numerous immature individuals of different ages pertaining to most of, or in some cases all, the above five castes. Besides the legitimate occupants of a termite habitation, there are to be found symbionts and inquilines belonging not only to other orders of insects but also to different classes of arthropods. It is evident, therefore, that the study of termite associations involves problems of the widest biological significance and, it may be added, an extensive field for research awaits those investigators who may be located in favoured countries.

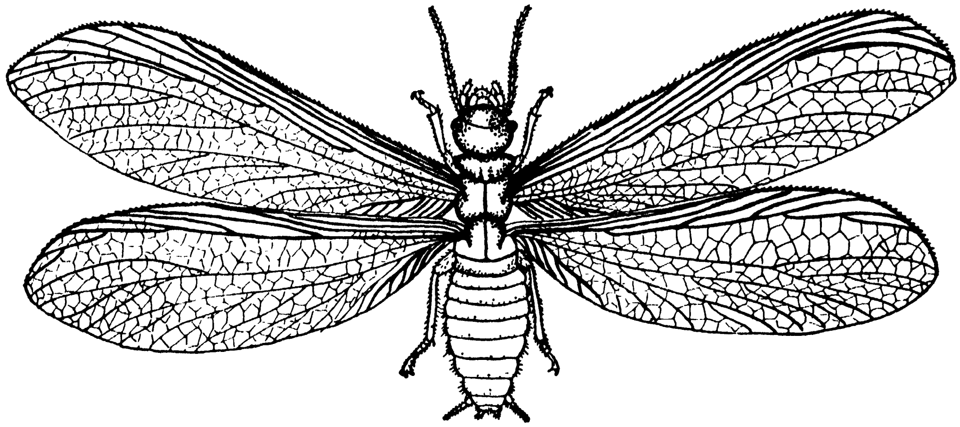

FIG. 272.—A WINGED TERMITE (*Archotermopsis*), MALE.

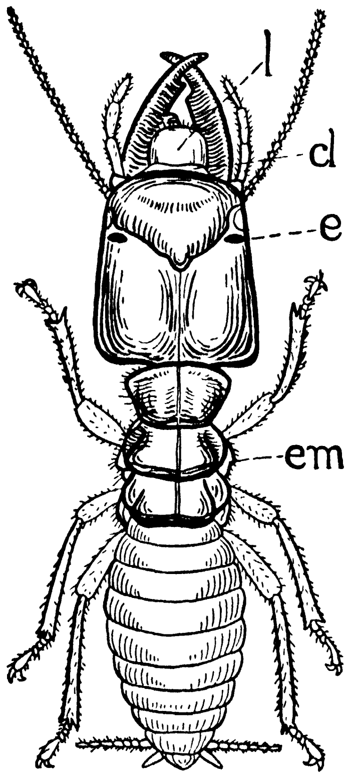

FIG. 273.—A SOLDIER TERMITE (*Archotermopsis*), MALE.
cl, clypeus; *e*, eye; *em*, epimeron; *l*, labrum.

External Anatomy.—The *cuticle* in termites is thin and flexible and, in the apterous castes, only that of the head is at all hard while the covering of the abdomen is frequently of the nature of a delicate translucent membrane. The aerial winged forms are more completely chitinized than any other caste; as a rule, the cuticle is more darkly coloured in species which either forage in daylight, or inhabit wood above ground than in subterranean forms. The *head* in the reproductive castes and workers is ovoid or rounded, while in the soldiers it is much larger and more often oblong or pyriform (Figs. 273, 274): in the latter caste it may exceed in size the whole of the rest of the body. The median and V-shaped *epicranial sutures* are frequently evident although extremely variable in their degree of development. *Compound eyes* are universally present in the macropterous forms, but suffer reduction to a greater or lesser extent in the other reproductive castes. They may be present in all castes of species which live or forage above ground, and are hence more exposed to daylight, but when present in the soldiers and workers they almost invariably exhibit degeneration. *Ocelli* are frequently present but do not occur unless accompanied by compound eyes: the median unpaired ocellus is wanting. The *antennæ* are moniliform and arise from shallow fossæ situated immediately above the base of each mandible. The number of joints varies from about 9 or 10 to over 30, being greatest in some of the more primitive genera; it also varies according to the caste and age of the individual and is highest in the macropterous forms. After emergence from the egg, the antenna increases in length by means of the intercalation of new joints, through the growth and subdivision of the third joint, and those joints directly derived from it. The *labrum* is well developed and largely overlies the bases of the mandibles. It is extremely variable in form (Fig. 274) and is hinged to the *clypeus*. The latter sclerite is divisible into a chitinized *post-clypeus*, which is firmly fused with the frons, and a more membranous distal portion or *ante-clypeus*.

The mouth-parts (Figs. 274, 275) closely resemble those of the Orthoptera in their general features. The *mandibles* in the reproductive forms and workers are very similar and present few striking deviations in form. In the soldiers, on the other hand, they are exceedingly variable in different genera, often attaining a great size (Fig. 274), accompanied by curious anomalies of shape: among the nasute soldiers, however, they are vestigial and minute. The *maxillæ* only differ in points of detail throughout the order. The galea is hood-like and commonly 2-jointed: the lacinia is strongly chitinized, and powerfully toothed distally, becoming more or less laminate basally, and is armed with stout setæ along its inner margin: the palpi in all cases are 5-jointed. The *labium* possesses a large basal plate which has received various names and may be termed the *postmentum*, or undifferentiated mentum and submentum (Fig. 13). Anteriorly it bears the *prementum* which is of a generalized type. The latter region exhibits more or less evident traces of a paired origin and carries both glossæ and paraglossæ. The *hypopharynx* is always large and is very similar to that of the Orthoptera; *superlinguæ* are wanting, unless a pair of minute chitinized sclerites are to be regarded as their counterparts.

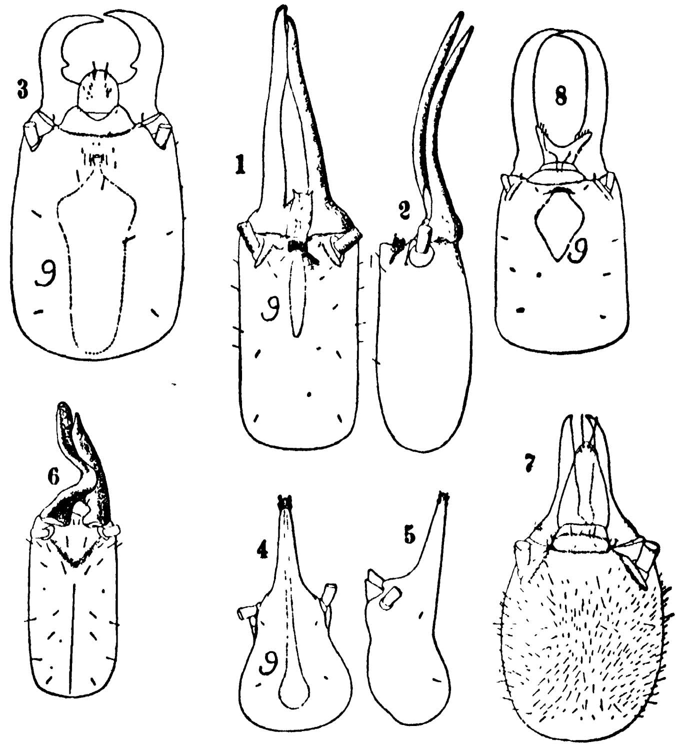

FIG. 274.—HEADS OF SOLDIERS OF AFRICAN TERMITES.

1, 2, *Mirotermes*. 3, *Hamitermes*. 4, 5, *Eutermes*. 6, *Pericapritermes*. 7, *Microtermes*. 8, *Cubitermes*; g, frontal gland. *After* various figures by Silvestri, *Boll. Lab. Zool. Portici*, 9.

In the *cervicum* there are two pairs of large and conspicuous lateral cervical sclerites, those of a pair being placed at right angles to one another: vestigial dorsal and ventral sclerites are also sometimes present.

In the *thorax* the terga are well developed: the pronotum is the most distinct, its many variations in form affording generic characters. It may be flattened and shield-like, heart-shaped, laterally lobed or very often saddle-shaped. The *meso-* and *meta-notum* are of very nearly equal size and much less variable or pronounced in character. On the ventral surface, the sterna are membranous with their boundaries often difficult to distinguish. The *prosternum* is greatly reduced and definite shields are often wanting; in *Archotermopsis* it consists of two small triangular plates which are separated from one another in the median line. The *mesosternum* is the largest of the three sterna and is a variably shaped shield; articulating with it posteriorly is a small rod-like *mesosternellum.* The *metasternum* is very wide and partially hidden from view by the bases of the middle pair of legs: a *metasternellum* is likewise present. In each segment the sides of the sternum are separately chitinized to form laterosternites which also articulate with the *episterna.* The latter elements in the prothorax are strongly chitinized bands which pass upwards to articulate with the under surface of the pronotum on either side. In the meso- and meta thorax the episterna are large, and in the macropterous form reach the bases of the wings. The three pairs of *legs* are very similar: at their bases the epimera are well developed and the *coxæ* very large and broad. In the middle and hind pairs a *meron* is marked off from the rest of the coxa by means of a deep suture. The tibiæ are long and slender: among the most primitive genera they are armed with both terminal and lateral spines, but in the majority lateral spines are wanting. The tarsi are typically 4-jointed: the only exceptions are *Mastotermes* which has 5 complete joints. In *Archotermopsis* and its related genera, *Termopsis* and *Hodotermopsis,* the tarsi are imperfectly 5-jointed, the 2nd joint being reduced. In the winged imagines of *Mastotermes,* and also of *Archotermopsis,* and other Calotermitidæ, an *empodium* is present between the claws of the feet; in other families this structure is wanting.

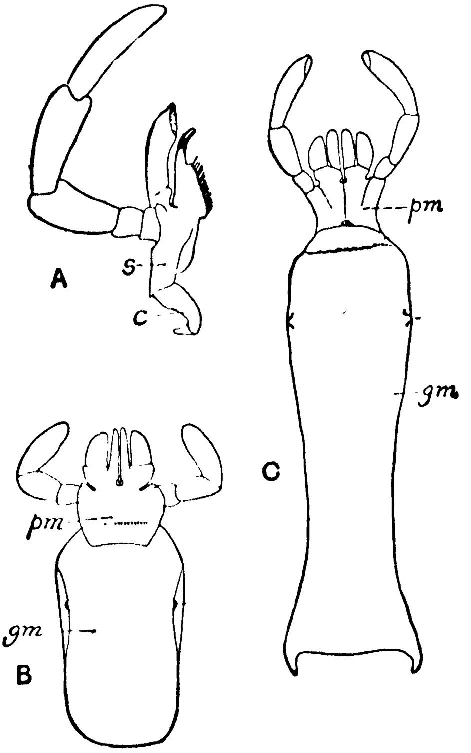

FIG. 275.—*ARCHOTERMOPSIS.*

A, maxilla of soldier B, labium of macropterous form. C, labium of soldier; *c,* cardo, *gm,* postmentum; *pm,* prementum; *s,* stipes.

The *wings* (Figs. 276, 277) of termites are characterized by the essential similarity in size, form, and venation of the two pairs of those organs. The veins of the anterior portion of each wing are strongly chitinized, while those distributed over the remaining area are much less pronounced and exhibit indications of degeneration. This feature has probably resulted from the slight use to which the wings are subjected, more durable organs being unnecessary. There is a striking absence of regular cross-veins, and the wing-membrane is stiffened in many cases by the presence of an irregular slightly chitinized network between the veins. The veins distributed over the intermediate region of the wing are reduced to faint lines while, on the other hand, there is a large posterior group of accessory veins borne by the cubitus. The venation (vide Comstock; also Fuller 1919) is primitive in a few genera (*Mastotermes, Archotermopsis, Termopsis*), but in the remainder of the order specialization by reduction is evident, affecting more particularly the radial and median veins. In the fore-wing of *Mastotermes*, according to Comstock, there is no true costal vein : Sc is 2-branched, and R_{1-5} are recognizable as separate branches. Both M and Cu are well developed, but there are no anal veins, their place being taken by several accessory branches of Cu. In the hind-wing Sc is unbranched, R_1 is absent, and M arises from the stem of R_{4+5}. Three anal veins are present and support a well-developed anal lobe (Fig. 296). The presence of the latter feature recalls the Blattid hind-wing and is a primitive character found in no other termites. *Archotermopsis* and *Termopsis* exhibit the first stage in reduction, R_{2+3} being undivided in the fore-wing, and the anal lobe in the hind-wing being vestigial. In *Leucotermes*, and the higher Isoptera, the costal margin is greatly thickened through the fusion of certain of the anterior veins, R is represented by a single stem, possibly R_{4+5}. M usually retains one or more branches, and the remainder of the wing is occupied by the accessory branches of Cu. One of the most striking features of the termite wing is the presence of the *basal* or *humeral suture* which is a line of weakness along which the fracture and shedding of the wings takes place. The stump of the wing, or that portion which lies between the humeral suture and the thorax, persists throughout life and is commonly termed the *scale*. This property of casting the wings is not entirely confined to the Isoptera. In the Blattid *Panesthia* the wings are torn off in a somewhat irregular manner in a certain proportion of individuals ; in the Zoraptera (vide p. 300) they are likewise shed but the fracture is more regular although no basal suture is developed.

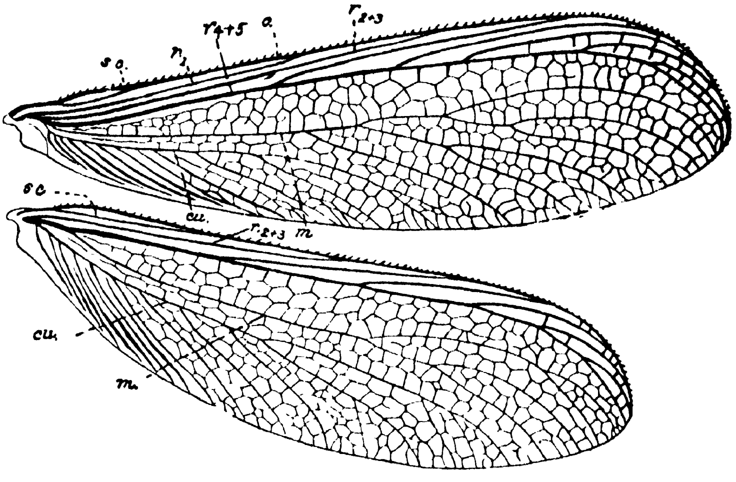

FIG. 276.—FORE AND HIND WINGS OF *ARCHOTERMOPSIS*.

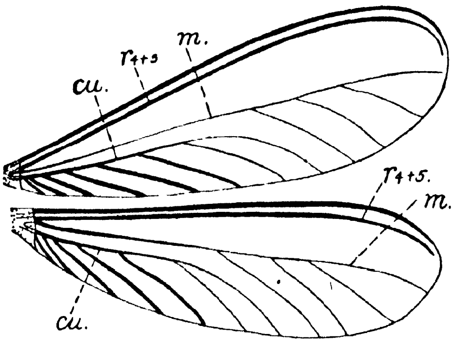

FIG. 277.—FORE AND HIND WINGS OF *EUTERMES* SP.

The *abdomen* is 10-segmented, the full number of terga being present. The first sternum is atrophied and the sternal plates differ markedly in the two sexes of the reproductive forms. In the males of many termites all the sterna are entire : in certain of the higher forms (*Eutermes*), however, the 9th sternum is divided. In the females the 7th sternum is greatly enlarged forming the subgenital plate which overlies the succeeding sterna. The terminal segment of the abdomen carries a pair of short *cerci* which are present in all castes. In *Archotermopsis* they are composed of 6–8 joints, in *Mastotermes* and *Termopsis* of 5 joints, *Hodotermopsis* 3–6 joints, while in the family Termitidæ they are, for the most part, reduced to the condition of 1- or 2-jointed tubercles. On the hind border of the 9th sternum a pair of small, unjointed *anal styles* are frequently present. They occur in both sexes of the soldiers and workers and in the nymphs of all castes: in the reproductive forms, with rare exceptions, they are present in the males only. External sexual differentiation is clearly evident in the soldiers and workers of *Mastotermes, Archotermopsis,* and a few other primitive forms. In the two first mentioned genera there is a similar differentiation of the terminal ventral plates as in the sexes of the reproductive forms. A reduced ovipositor of the Blattid type is present in *Mastotermes.*

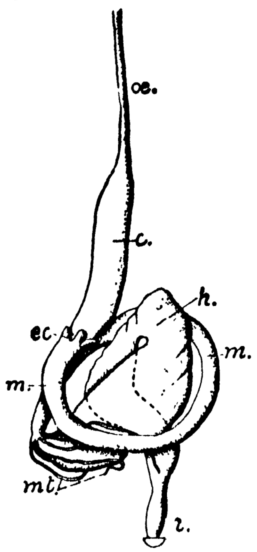

FIG. 278.—*ARCHOTERMOPSIS*, ALIMENTARY CANAL OF SOLDIER.

œ, œsophagus; *c*, crop; *ec*, enteric cœca; *m*, mid-intestine; *mt*, Malpighian tubes; *h*, hind-intestine; *r*, rectum.

Internal Anatomy.—The *digestive canal* (Figs. 278, 279) is a coiled tube of moderate length and exhibits comparatively few important variations in structure. The mouth leads into an elongate *œsophagus* of narrow calibre which expands distally to form the *crop*. The latter organ is seldom capacious and frequently is only slightly emphasized. It is followed by the *gizzard*, provided with an armature of chitinous denticles: this organ is simple and ring-like in certain of the more primitive forms, becoming more pronounced among other termites. Beyond the gizzard the fore-intestine protrudes into the cavity of the stomach forming a large *œsophageal valve*. The stomach is tubular, of uniform calibre throughout and often completely encircles the hind-intestine. At the junction of the stomach with the latter region are the *Malpighian tubes*; these are variable in number, eight being usually present in the Calotermitidæ and from two to eight among the Termitidæ. In *Archotermopsis* five *enteric cœca* arise as outgrowths from the anterior end of the stomach; in *Capritermes* Holmgren (1909) mentions a pair of large berry-like glands arising near the origin of the Malpighian tubes. At its commencement, the *hind-intestine* is a short narrow tube (or ileum), often separated by means of a valve from the *colon*. The latter region is usually an extensive chamber which, in the wood-feeding termites, is frequently distended owing to the presence of large numbers of Protozoa. The *rectum* is a narrow tube of very variable length and terminates in an ovoid or spherical chamber opening to the exterior by means of the anus.

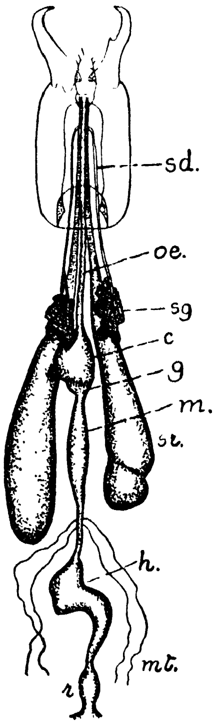

FIG. 279.—*TERMES CEYLONICUS*, ALIMENTARY CANAL OF SOLDIER.

g, gizzard; *sd*, salivary duct with gland *sg* and reservoir *sr*. Other lettering as in Fig. 264. *After* Bugnion, *Rec. Suisse Zool.*, 1911.

Salivary glands are well developed and racemose in character; each gland is provided with a salivary reservoir. The ducts, both from the glands and their reservoirs, eventually unite to form a common salivary canal opening at the base of the hypopharynx. Bugnion (1911) states that in the soldiers of *Termes ceylonicus* Wasm. the salivary glands are very large and secrete a viscous milky fluid probably defensive in function.

The *circulatory system* has been very little investigated; the *heart* consists as a rule of 8–10 chambers and is prolonged anteriorly as the *aorta* which communicates with the cephalic blood space just behind the brain.

The *fat-body* is more extensively developed in the reproductive forms than in the soldiers or workers. Feytaud (1912) states that in the kings and queens this tissue undergoes a complete change several years after swarming. Migratory cells ("leucocytes") enter it in large numbers and undergo division, gradually building up a new fat-body at the expense of the old. In the course of its development the new tissue often assumes a regular columnar form which is lost when it becomes actively functional.

The *nervous system* presents no notable variations, excepting differences in the degree of development of the brain and eyes in the reproductive and sterile castes. In the ventral nerve cord there are three thoracic and six abdominal ganglia. The sympathetic system is well developed and closely resembles that of the Orthoptera.

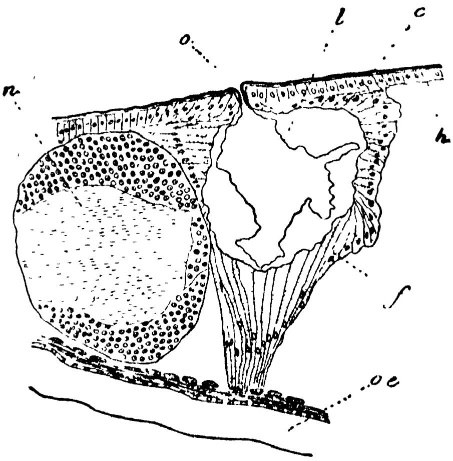

FIG. 280.—*Reticulotermes lucifugus*, SECTION OF FRONTAL GLAND OF MACROPTEROUS FORM.

c, cuticle of head; *f*, frontal gland; *h*, hypodermis; *l*, chitinous lining of gland; *n*, brain; *o*, frontal pore; *œ*, œsophagus. *After* Feytaud.

The *frontal gland* (Fig. 280) is a very characteristic termite organ and is formed by a differentiation of a group of hypodermal cells in the median line of the frons. It may be present in all castes but usually attains its greatest development in the soldiers (vide Holmgren, 1909; Feytaud, 1912; Thompson, 1916 and 1917). In its completely developed condition it is a sac-like gland which communicates with the exterior by means of the *frontal pore*. The latter opens in a shallow depression of the surface of the head where the chitin is pale-coloured and known as the *fontanelle*. The gland is, furthermore, connected with the brain by a median *fontanelle nerve*. In *Leucotermes* (*Reticulotermes*) the gland is well exhibited in an average degree of development. According to Feytaud in the macropterous caste of *L. lucifugus* it is a spherical sac, which opens to the exterior, and is lined by a chitinous membrane; beneath the latter is a layer of elongate epithelial cells. In the soldiers its configuration is very similar, but the gland is somewhat larger, while in the workers it is rudimentary, being merely represented by a group of hypodermal cells and devoid of a frontal pore. Thompson has made a more detailed study of the organ in *L. flavipes* and states that in this species it is largest in the macropterous caste. It is present in the newly hatched nymphs, although barely recognizable, and undergoes differentiation as development proceeds. The gland attains its greatest development in the soldiers of *Arrhinotermes* and *Coptotermes*; in these genera it is in the form of an extensive sac, reaching backwards to the extremity of the abdomen (Fig. 289), and discharges a milky latex-like secretion through an enlarged frontal pore. In the soldiers of *Mirotermes* the gland opens at the apex of a prominent *frontal tubercle*, and in the nasute soldiers of *Eutermes* the tubercle is prolonged into an elongate rostrum, through which the duct of the gland passes.

The nature and function of the secretion of the frontal gland is problematical: in some cases it appears to have defensive significance while in others the gland is so little developed as to appear to be non-functional. Thompson suggests that the frontal gland arose phylogenetically from the original median ocellus which is now wanting in termites. This view is based upon the position and the structural resemblances of the frontal gland and lateral ocelli, upon the presence of the fontanelle nerve in the same frontal section in which the lateral ocellar nerves enter the brain, and upon the resemblance of the cells of the gland in developing nymphs to visual cells. Facts enumerated by Holmgren bearing upon the morphology of the frontal gland and the phylogeny of termites, are also regarded by Thompson as lending support to this view.

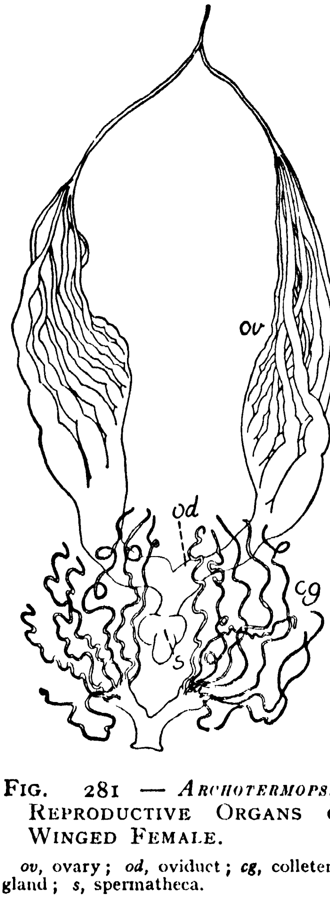

FIG. 281 — *ARCHOTERMOPSIS*, REPRODUCTIVE ORGANS OF WINGED FEMALE.

ov, ovary; *od*, oviduct; *cg*, colleterial gland; *s*, spermatheca.

The *sexual organs* attain their complete functional development in the reproductive castes. In the soldiers and workers they are almost always aborted to a greater or less degree. Exceptions are met with, however, in *Archotermopsis* whose soldiers have fully developed sexual organs, which are evidently capable of functional activity, and Heath records members of this caste in *Termopsis* producing fertile eggs. Almost every grade in degeneration of the sexual organs can be traced among the soldiers of various genera, until the culminating point is reached in *Eutermes monoceros* Koen. where, according to Bugnion (1909), no traces of these organs are to be found. In the reproductive castes (Fig. 283), the *testes* are simple and consist of a variable number of short digitate lobes (usually about 8–10) situated in or near the 8th abdominal segment. The *vasa deferentia* are a pair of short tubes which converge and unite to form a muscular *ejaculatory duct*. At the point of union there is a pair of

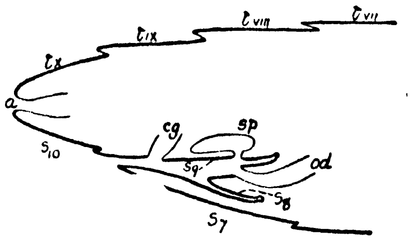

FIG. 282.—*ARCHOTERMOPSIS*, DIAGRAMMATIC SECTION OF THE APEX OF THE ABDOMEN OF A FEMALE SOLDIER.

t_{vii-x}, terga; s_7–s_{10}, sterna; *a*, anus; *cg*, opening of colleterial glands; *sp*, spermatheca; *od*, oviduct.

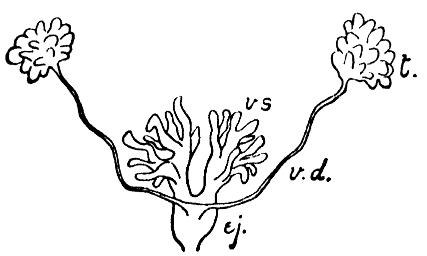

FIG. 283.—*ARCHOTERMOPSIS*, REPRODUCTIVE ORGANS OF WINGED MALE.

t, testis; *v.s.*, vesicula seminalis; *vd*, vas deferens; *ej*, ejaculatory duct.

vesiculæ seminales, each consisting of a group of small tubuli. Accounts are conflicting with regard to the nature of the spermatozoa and further investigation is needed. According to Grassi and Sandias (1897) the spermatozoa in *Calotermes flavicollis* are non-motile and devoid of the usual tail. In *Archotermopsis*, however, they do not offer any exceptional features and the latter appendage is present. In the female (Fig. 281), each *ovary* consists of an extremely variable number of panoistic *ovarioles* (30–45 in *Archotermopsis*) which open separately into the oviduct. The two oviducts communicate by means of a common aperture with the genital pouch whose floor is formed by the enlarged 7th sternum (Fig. 282). The dorsal wall of the pouch receives the apertures of the *spermatheca* and the common duct of the colleterial glands. The latter organs consist of a large number of elongate and much convoluted tubuli, whose function has not been ascertained.

The Castes of Termites

It has been previously mentioned that termites live together in large communities composed of polymorphic individuals. The latter are divisible into three castes of reproductive forms and two of sterile forms (Vide Grassi and Sandias, 1897: Snyder, 1920).

The **Reproductive Castes** consist of—(1) The MACROPTEROUS FORMS (Fig. 272). The members of this caste are the winged imagines of most authors and the "adults of the first form" of Thompson (1917). They are to be regarded as the ancestral caste among termites from which the other forms, both fertile and sterile, have been derived. The two pairs of large membranous wings, nearly equal in size, afford the character upon which the name Isoptera is based. The body in these individuals is well chitinized and often darkly coloured, compound eyes are fully developed, and there are frequently paired ocelli. The caste is adapted for a brief aërial life and its members are concerned with the foundation of new colonies. The brain is large, the frontal gland when present is relatively well developed, and the sexual organs attain a greater size than in any other caste. (2) The BRACHYPTEROUS FORMS ("adults of the second form," Thompson). The members of this caste live a subterranean life, the body is much less chitinized than in the macropterous form, and is straw-coloured or greyish white.

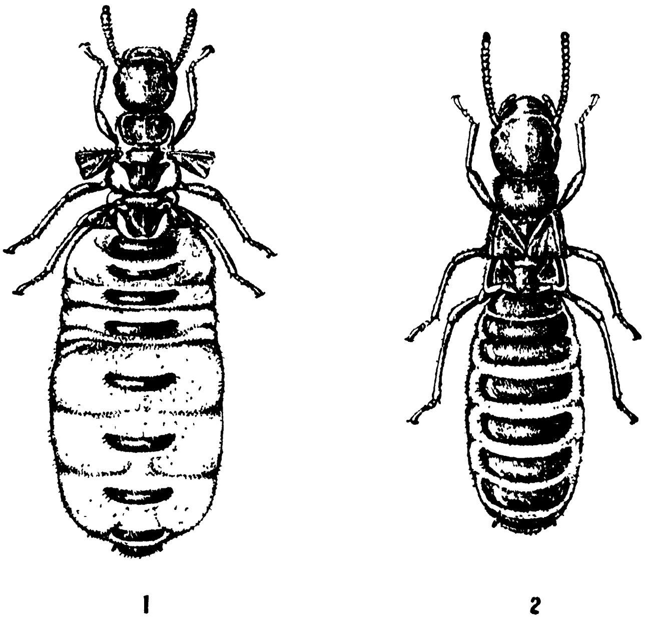

FIG. 284.—*Reticulotermes flavipes.* Dealated Queen (1) and King (2) of Macropterous Form.
After Banks and Snyder, *U.S. Nat. Mus. Bull.* 108.

Growth of the wings is inhibited, these organs remaining in a more or less nymphal condition and in the form of short scale-like vestiges, but usually with a distinct venation (Fig. 285). The compound eyes are smaller and less strongly pigmented than in the previously mentioned caste: the brain, frontal gland, and sexual organs are also somewhat reduced in size. The function of the brachypterous forms is not fully understood, and the question whether they are merely useful to the individual colony in maintaining its numerical strength, or are of importance to the species in founding new colonies, needs investigation. (3) The APTEROUS FORMS ("adults of the third form," Thompson). This caste is a comparatively rare one and does not appear to have been met with among the higher termites, i.e. — the Termitidæ. Its members are subterranean in habits, there is an almost complete absence of coloration in the cuticle, the compound eyes are vestigial and there is a complete absence of wings (Fig. 285). The caste has been studied in detail in *Leucotermes* (*Reticulotermes*) and *Prothinotermes* by Thompson and Snyder (1920) who point out that although it bears a close resemblance to the workers of these termites it may be distinguished by certain definite characters. The conditions under which the apterous forms are present and exercise their full reproductive capacity are not understood.

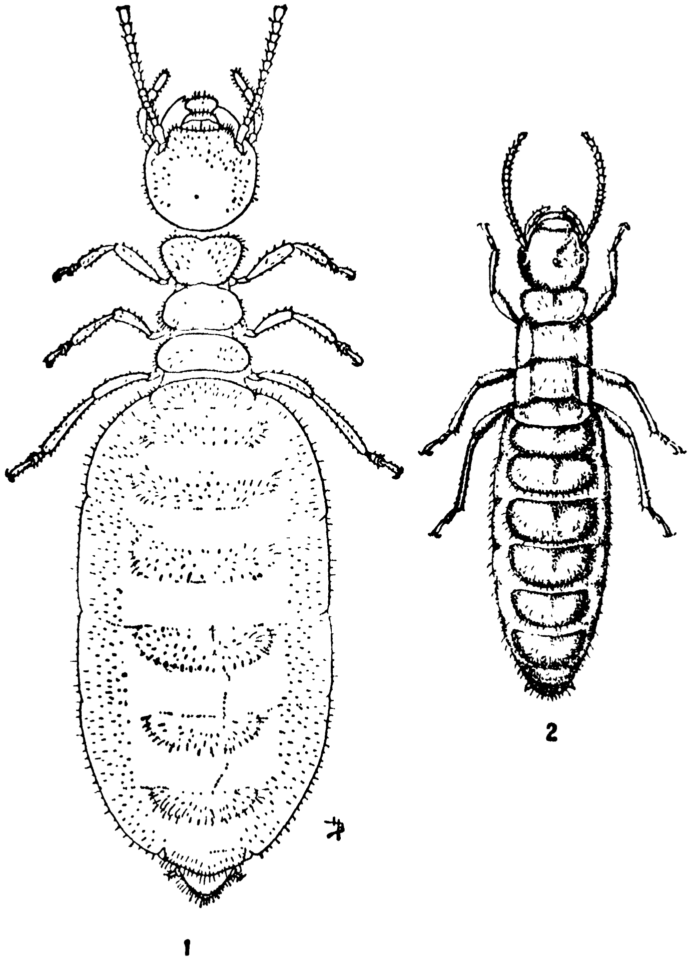

FIG. 285.—1, *Reticulotermes flavipes*, Apterous Queen. 2, *R. virginicus*, Brachypterous Queen.
After Banks and Snyder *loc. cit.*

According to Grassi and Sandias (1896–97) the brachypterous and apterous forms are "substitute" or "complementary" neoteinic castes, which functionally replace the macropterous forms in cases of necessity, and under certain conditions. The gonads mature earlier in these castes than in the macropterous forms and this fact, together with their general nymphal appearance, has led the Italian observers to regard them as immature forms. They maintain that the latter could be induced, at the will of the colony by extrinsic means, to undergo precocious sexual development. The pale coloration and weak chitinization, together with the reduction of the visual organs, are features correlated with subterranean or concealed habits and are not necessarily associated with immaturity. Furthermore, adult brachypterous and apterous forms are well known in certain other orders of insects, while the usual absence of anal styli, in the females of these two castes, suggests the probability that the latter are composed of adult rather than of neoteinic individuals.

The reproductive castes exhibit a remarkable postmetamorphic growth which is initiated as a response to the stimulus exercised by the developing sexual organs after coitus has been effected. The fertilized females, or queens, of the more primitive genera betray this postmetamorphic growth only to a very slight degree: on the other hand, among the Termitidæ they attain relatively enormous dimensions (Fig 294). These gigantic queen termites often attain a length of 5 to 9 cm. or more: they have attracted the wonder of generations of naturalists, and the appetite of the savage who has prized them as a food delicacy. Although queens may be developed from all three reproductive castes, they attain the largest dimensions when derived from the macropterous form. Such queens are easily recognizable on account of the persistent bases of the cast-off wings (Fig. 284). The increase in size only directly affects the abdomen, the head and thorax remaining unchanged in appearance, forming a mere appendix to the greatly distended hind-body. The vast size of the latter is mainly due to the increased development of the ovaries and fat-body. The postmetamorphic growth does not affect the size of the external sclerites but, on the other hand, the intersegmental membranes develop to such a degree that they constitute almost the whole abdominal covering, leaving the original tergal and sternal plates as small islands of chitin.

The changes undergone during postmetamorphic growth have been studied by Feytaud (1912) and Bugnion (1912): the chief features of the process may be summarized as follows. The wing-muscles, which occupy the greater part of the thoracic cavity, degenerate and are broken down, partly by phagocytic action. The original fat-body, as mentioned earlier in the present chapter, undergoes complete transformation, being replaced by a new tissue. Certain changes supervene in the digestive system in conformity with an alteration in diet. The queen no longer partakes of ligneous or other hard matter but is nourished upon saliva or, in the fungus-growing species, upon fungal hyphæ in combination with that secretion. The jaw-muscles in consequence become reduced in size and power: the stomach undergoes correlated changes, both structural and functional, the Malpighian tubes increase in length, while the hind-intestine suffers marked curtailment. The volume of the blood-tissue is greatly increased, while the nervous system and dorsal vessel undergo elongation in conformity with the general extension of the abdomen. The most striking changes are exhibited in the reproductive system which monopolizes, as it were, the greater part of the abdomen and converts the queen into one vast, inert, egg-laying mechanism. The changes involved are those of size and, in its general morphology, the reproductive system of the queen does not differ from that of the same individual when in the winged stage: in *Termes redemanni* Bugnion mentions that one ovary alone consisted of the enormous number of 2,420 ovarioles.

The **Sterile Castes** (Figs.273, 286) are divisible into workers and soldiers. These are apterous individuals in which the sexual organs are arrested in their development or atrophy, and are consequently non-functional.

(1) The WORKERS are numerically the most important members of the termite community. They are usually pale coloured with the integument but little chitinized, and they bear a closer resemblance to the nymphs than to the adult members of other castes. Except in the primitive genus *Mastotermes*, external sexual characters are usually absent. The head of the worker is directed downwards, it is relatively wider than in the reproductive castes, but never attains the dimensions found among the soldiers. Compound eyes are usually absent, but in certain species they are present in a vestigial condition ; tolerably well developed faceted eyes occur in the workers of *Hodotermes*, which are active above ground during daylight. The mandibles resemble those of the reproductive castes but they are more powerful and adapted for gnawing wood and other vegetable tissue. In the configuration of the thorax the workers resemble the soldiers rather than the imagines. On the whole, distinctive characters are but little emphasized among the workers of the various species and, for this reason, it is usually a matter of great difficulty, or an impossibility, to determine their specific identity unless members of other castes are taken with them at the same time.

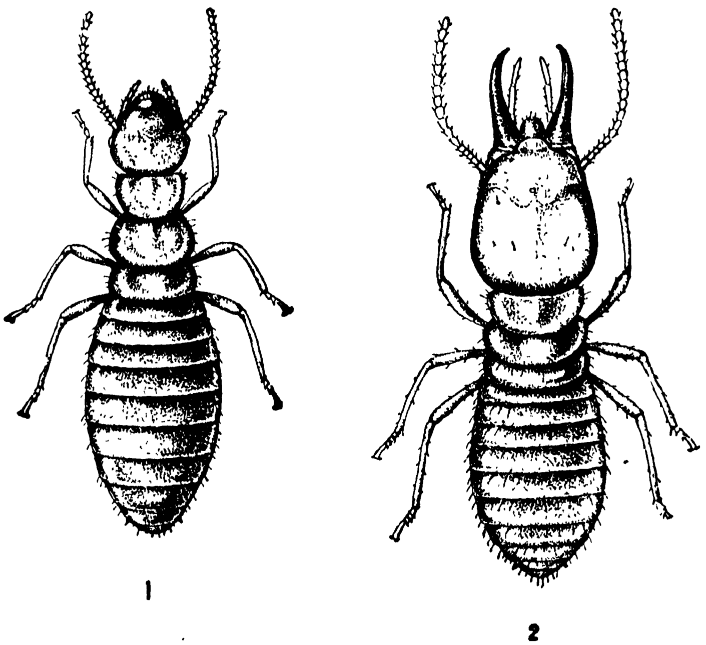

FIG. 286.—*PRORHINOTERMES SIMPLEX.* 1, worker ; 2, soldier. *After* Banks and Snyder, *U.S. Nat. Mus. Bull.* 108.

Not infrequently the workers are dimorphic, being divisible into major and minor forms. In such cases the head and mandibles, and often the body, of the major workers are distinctly larger than those of the minor individuals. In some species, however, it is impossible sharply to separate the workers into these two classes owing to the occurrence of numerous intermediate forms. Dimorphism among workers occurs, for example, in *Termes* (*Macrotermes*) *estheræ* Desn., *Odontotermes obesus* (Ramb.), *O. redemanni* Wasm., *O. horni* Wasm. and in many species of the genus *Eutermes*.

Although taking no part in reproduction, and seldom any part in the defence of the community to which they belong, practically all other duties devolve upon the members of this caste. They exhibit marked care for the eggs and young and, in times of danger, may remove them to situations which afford greater safety. They also feed and tend the queens, forage for food, often at a distance from the nest and, in the fungus-growing species, attend to the cultivation of these lowly forms of vegetation which they plant in special chambers. In the case of lignicolous species, the workers excavate the galleries and tunnels which serve for the nest ; in the mound-building forms they construct the termitarium, and repair any injuries sustained by the latter. Owing to their gnawing propensities the workers have earned for termites their unenviable reputation as destroyers of crops, woodwork and other materials serving the convenience of man. There is no true worker caste in *Archotermopsis*, its functions being performed by the nymphs of the soldiers and sexual forms. The worker caste is likewise absent in *Termopsis* and a few other primitive genera.

The SOLDIERS are the most specialized members of the termite community and appear to be wanting only in the genus *Anoplotermes*. They may be readily recognized by the great size and strong chitinization of the head. The mandibles also attain much larger dimensions than in other castes, and frequently assume striking or almost grotesque forms (Fig. 274). Two well-defined types of soldiers can be distinguished—(*a*) the mandibulate type with large and powerful jaws but no frontal rostrum; (*b*) the nasute type (Fig. 287) in which there is a median frontal rostrum but the jaws are small or vestigial. Soldiers conforming to either of these types may frequently be separated into major and minor forms as in the workers, and often in the same species. In other instances trimorphism obtains, large, intermediate, and small soldiers occurring within the limits of a single species. In certain other cases, however, the soldiers are extremely variable and, although separable into large and small forms, the two extremes are connected by numerous individuals of intermediate sizes.

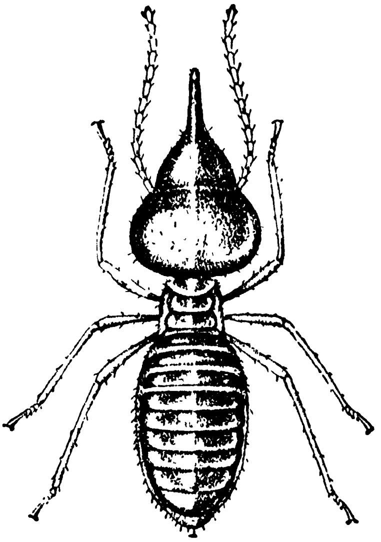

FIG. 287.—*Eutermes costaricensis* Nasute Soldier.
After Banks and Snyder, *loc cit.*

As in the workers, the soldiers consist of both males and females but, except in those of *Mastotermes*, *Archotermopsis* and certain species of *Calotermes*, external secondary sexual characters are slight, and the sex of the individual can be best ascertained from an examination of the gonads. Tolerably well developed faceted eyes occur in the soldiers of *Hodotermes*, and vestigial eyes are found in those of *Archotermopsis*, *Calotermes* and other genera, but more often than not visual organs are totally wanting: a pair of reduced ocelli may also be present. The antennæ usually consist of one or several joints less than in the reproductive castes.

Although numerous modifications are exhibited in the form of the head and mandibles among soldiers of various species, comparatively few of these differences can be interpreted as being special adaptations to particular functions. The soldiers are mainly concerned with the defence of the colony which they protect by seizing or repelling any intruders. Means of defence are afforded, in many cases, by the great size and power of the mandibles: in others it resides in the capacity of the individual for ejecting a repellent fluid. When disturbed the mandibulate soldiers may often be observed to assume threatening attitudes with the jaws outstretched, and they will usually seize any object presented to them. Ants are among the bitterest enemies of termites, and the soldiers of the more courageous termites not infrequently seize them, and eject them when attempting to enter the nest. The highly specialized soldiers of some species are apparently of little service to the community. Those of *Capritermes*, for example, with their curiously twisted mandibles, are ill adapted for performing any utilitarian function. Any defensive rôle which such termites may possess would appear to be solely expressed in their general aggressive appearance and power of assuming threatening attitudes. In several species with exceptionally large heads the soldiers are stated to block up gaps in the walls of the nests, while the workers are undertaking repairs.

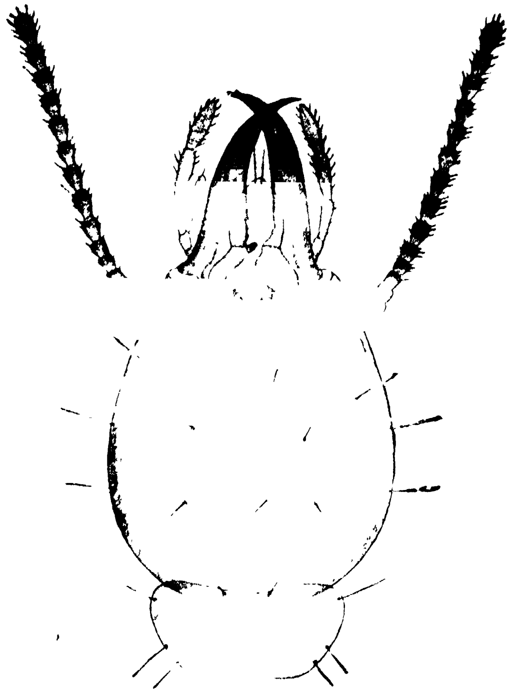

FIG. 288.—*COPTOTERMES CEYLONICUS*, HEAD OF SOLDIER SHOWING FRONTAL PORE.
After Bugnion.

In the second method of defence, referred to above, a viscid secretion is emitted through the frontal pore, situated in the anterior region of the head (Fig. 288). The possessors of this type of defensive capacity have as a rule small or vestigial mandibles, or the latter are ill-adapted for their usual function. In *Coptotermes*, a profuse white secretion is produced by an extensive gland occupying the greater part of the thoracic and abdominal cavities (Fig. 289). According to Holmgren a similar capacious gland is present in *Rhinotermes taurus*. In the nasute soldiers of *Eutermes* (Fig. 287) and other genera, the repellent secretion is the product of a retort-shaped glandular sac, situated in the head. A clear thick liquid is ejected through its duct which traverses the rostrum and opens at the apex of the latter. The soldiers of *Eutermes*, notwithstanding their small size, are usually not lacking in courage. When the nest is injured in any way, they issue through the broken parts in large numbers, and stand on guard while the workers are busily engaged in executing repairs. Globules of secretion may often be seen at the apex of the rostrum of the soldiers and this protective fluid appears to have a very

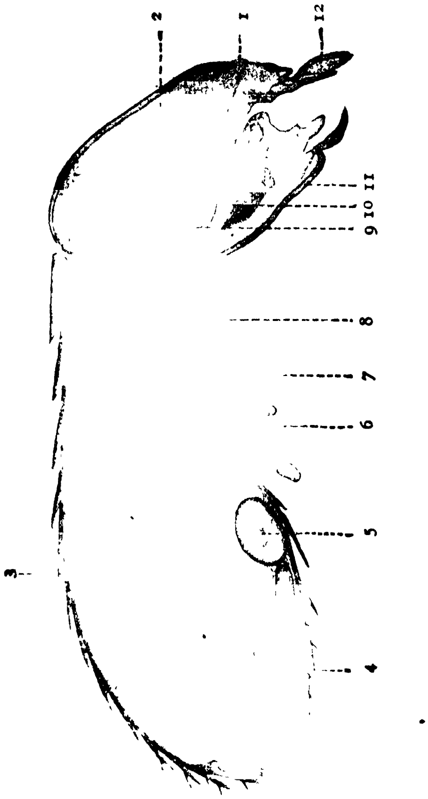

FIG. 289.—*COPTOTERMES CEYLONICUS*, MEDIAN LONGITUDINAL SECTION OF SOLDIER.

1, frontal pore; 2, 3, frontal gland; 4, hind intestine; 5, mid-intestine; 6, 7, 8, thoracic ganglia; 9, œsophagus; 10, sub-œsophageal ganglion; 11, mentum; 12, labrum. *After* Bugnion.

salutary effect upon any enemies. Haviland (1898) observed that the soldiers may be seen to eject a small quantity of the fluid on the antennæ of their foes : ants, he remarks, are rendered *hors de combat* by this means. In *E. triodiæ* Hill mentions that the secretion is ejected as a fine jet which has the appearance of a silken thread waving from the tip of the rostrum.

The Habitations of Termites

The simplest kind of termite habitation is found in the wood-feeding species, which usually lack the worker caste, and include the most primitive members of the order. *Archotermopsis* and *Termopsis*, for example, live in moist decaying trunks and logs of conifers. The abodes of such termites consist of nothing more than a series of galleries, excavated in the wood, without any external manifestation of their presence (Fig. 290). Other genera such as *Mastotermes, Calotermes, Neotermes* and *Cryptotermes* include species which bore into dry wood, often selecting posts and other structures, or furniture in buildings, as the seat of their habitations. *Calotermes militaris* and *C. greeni* are destructive to tea in Ceylon where they burrow in the stems of the bushes. *Rhinotermes, Leucotermes* (*Reticulotermes*) and *Coptotermes* live in the ground and infest wood indirectly through the soil. They are exceedingly injurious to any woodwork of buildings in contact with the ground. They also frequently issue above ground in order to obtain access to woodwork in their vicinity. With this object in view they construct covered passage-ways of earth, or fæcal matter, which enable them to work concealed from the light and from sundry enemies and, at the same time, surrounded by the requisite humidity. They are able, by means of these tubular communications, to pass from their underground chambers and reach the upper storeys of buildings or ascend lofty trees.

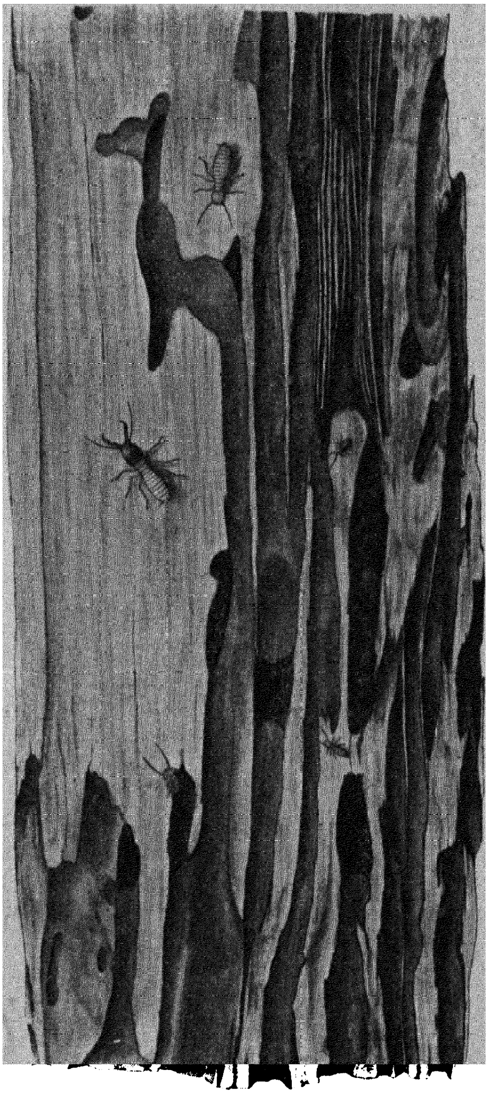

FIG. 290.—PORTION OF LOG OF *CEDRUS DEODARA* SHOWING GALLERIES OF *ARCHOPTERMOPSIS*. × ½.

In other cases very extensive structures known as termitaria (Figs. 291, 292) are constructed, particularly by the African and Australian species of the Termitidæ. These termite mounds are built of earth excavated in making subterranean chambers and were perhaps originally only a convenient method of disposing of this material. The outer walls and passages, and the royal cells of these habitations, are composed of earth particles cemented together to form a hard brick-like substance. The agglutinating fluid appears to consist either of saliva, or of the latter together with proctodæal matter. The inner galleries, where the brood is contained, are of a softer consistency, and are composed of woody or other comminuted material which has passed through the alimentary canal. Some of the most remarkable of all termitaria are the lofty steeple-like structures constructed by *Eutermes triodiæ* in Northern Australia. They are stated to exceed in size those of any known termite, and one recorded by Hill measured 20 feet high with a basal diameter of 12 feet. The greater bulk of the earth and sand used in their formation is collected on the surface, and not mined from below. The interior of such a termitarium presents a maze of irregular chambers and passages, and its walls are so resistant that it is difficult to make any impression upon them even with a sharp pick. The "compass" or "meridional" termite (*Hamitermes meridionalis*) is widely distributed in Aus-

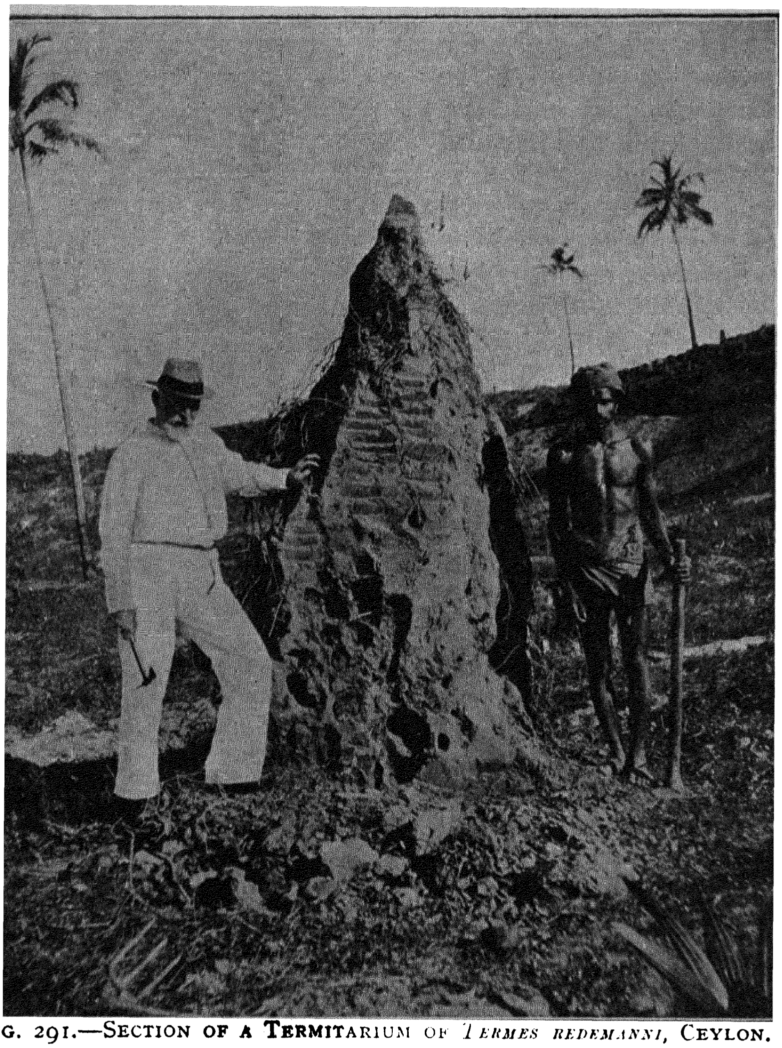

FIG. 291.—SECTION OF A TERMITARIUM OF *TERMES REDEMANNI*, CEYLON.
After Bugnion.

tralia. The habitations of this species may attain a height of 8 to 12 feet, and are flattened from side to side in such a manner that the broad sides face east and west, and the narrow ends north and south. It has been suggested that the reason for their being built according to this plan is in order to secure the maximum of desiccation, and to allow for the repairs, which are made during the wet season, being dried and hardened as speedily as possible.

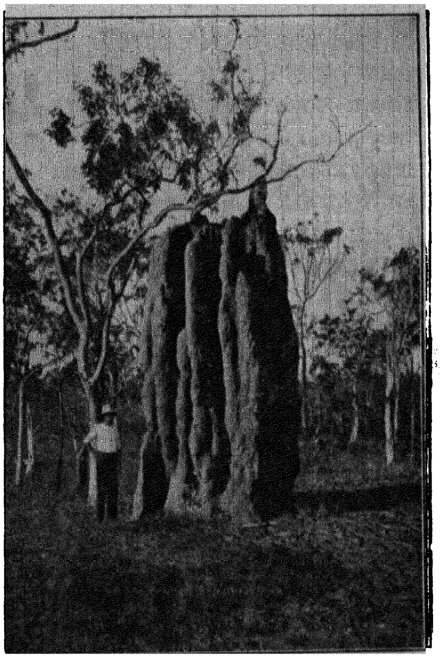

FIG. 292.—LARGE TERMITARIUM OF *EUTERMES TRIODIÆ*, AUSTRALIA.

After Hill, Proc. Linn. Soc. N.S.W., 1915.

Other species of termites live in the ground, without constructing termitaria above the surface, or only forming small mound-like structures (Fig. 293). Many termites which exhibit this habit are exceedingly injurious to the roots of grass, field crops, and other vegetation. Although the type of habitation may be very constant for a particular genus or species, in other cases considerable variation obtains. *Odontotermes*, for example, includes both mound builders and subterranean forms, and the two habits may be exhibited in the same species as in the common Indian termite *O. obesus*. Certain species of *Eutermes* construct gigantic termitaria of the type already referred to, while others form arboreal habitations often more or less spherical in form. The material used in constructing the latter appears to be comminuted wood, and the nest is composed of an outer envelope enclosing a comb-like mass of internal chambers. Such habitations bear a super-

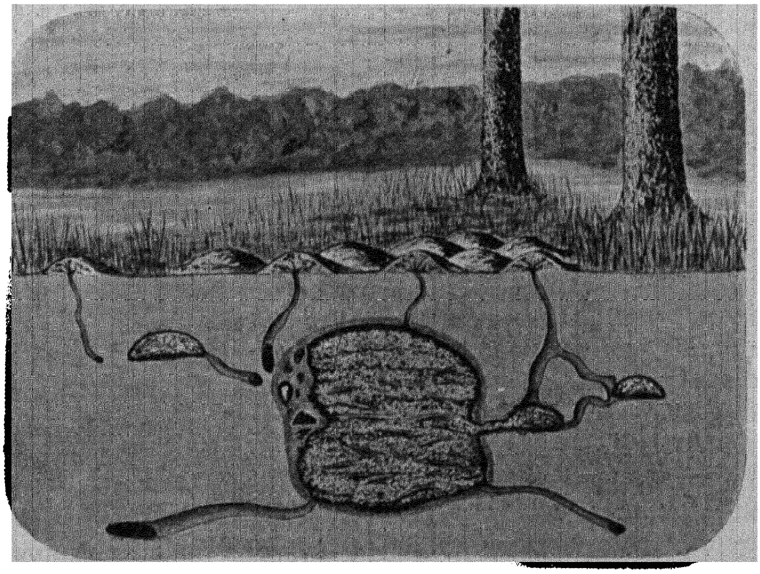

FIG. 293.—Vertical section of a nest of *Termes badius* (S. Africa), and perspective, showing trees crusted by termites with clay: small surface mounds and descending shafts: great cavity and supplementary cavities filled with fungus garden; queen-cell attached to wall of cavity (left side) and radiating galleries. × $\frac{1}{38}$. *After* Fuller, *Ann. Natal Mus.* 3.

ficial resemblance to the carton nests of arboreal Vespidæ. In many cases they are connected by means of covered passage-ways with subterranean abodes.

The rôle of subterranean termites has been compared by Drummond (" Tropical Africa ") with that of earthworms. By means of their underground activities they keep the soil in constant circulation, rendering it permeable to air and moisture. Also the fæcal matter of these insects serves to enrich the soil very much after the manner of the " casts " of earthworms. In many parts of the tropics there is scarcely a cubic yard of soil that is free from the burrows of these insects, and the number of individuals of the latter present defies all calculation.

The Termite Community and its Biology

The various castes which make up a termite community have already been described. In a typical colony of any of the higher termites the life of the community is dominated by the royal pair which consist of a deälated male and female. They are confined to a special royal cell which is usually deeply hidden in the recesses of the termitarium. The royal couple remain monogamous ; the queen attains relatively enormous dimensions (Fig. 294) and she is fertilized at intervals by the king. Among the most primitive termites there may be a number of these royal forms present : they are not necessarily located in permanent cells, and the queens do not exhibit the same great increase in bulk. It was formerly believed that if the original queen were destroyed the community would ultimately die out. This conclusion has been dispelled by the discovery of the brachypterous and apterous reproductive castes. Either one or both of the latter may be represented among the offspring of the original royal couple, and they eventually develop into new royalties which continue the population of

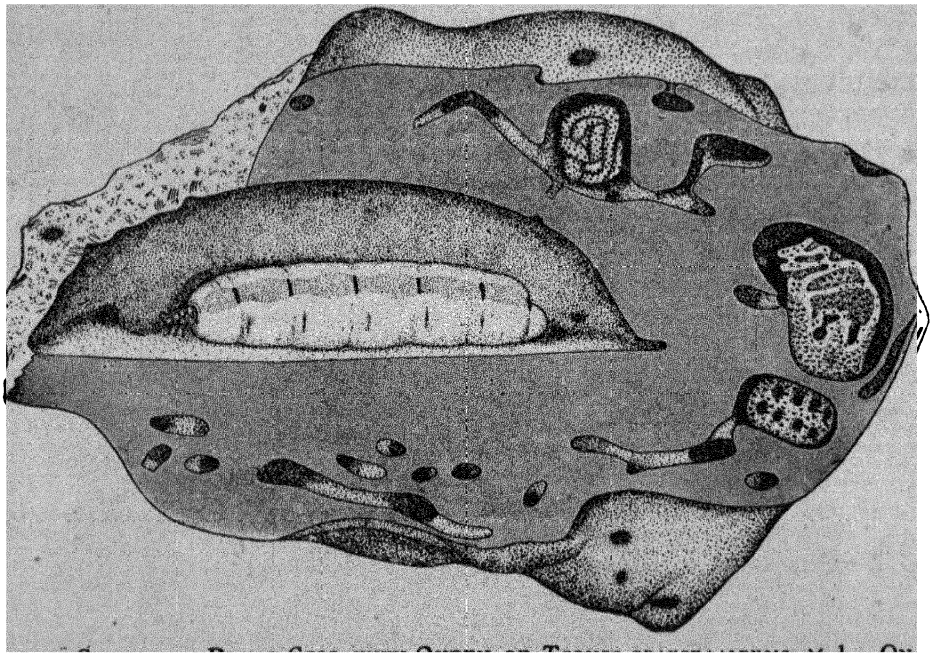

FIG. 294.—SECTION OF ROYAL CELL WITH QUEEN OF *TERMES TRANSVAALENSIS*, × ½. ON THE RIGHT CHAMBERS WITH FUNGUS GARDENS.

After Sjostedt.

the colony in cases of necessity. They are, moreover, polygamous, several kings being associated with a number of queens. Since it is evident that individuals representing two or three reproductive castes may coexist in the same community, the question arises as to the conditions under which these several castes may become functional. The macropterous forms, as will be referred to later, take to the wing and leave the habitation. There is no conclusive evidence, however, that the brachypterous or apterous reproductive castes regularly leave the colony to found new societies of their own and, in the presence of the original queen, they appear superfluous. It has been previously mentioned that Grassi and Sandias regard them as neoteinic forms, which are held in reserve so as to be brought into reproductive activity when occasion demands: Fritz Müller (1873) compared them with the cleistogamic flowers of certain plants. It has already been pointed out that the evidence for considering these two castes as being composed of neoteinic forms is not established, and that they are to be regarded as true adults. If the latter contention be correct, there appears to be nothing to prevent them from reproducing on their own account even when the original royal couple is present. It is, therefore, reasonable to conclude that they perform the double function of extending the colony, or of founding separate branch colonies, while the original queen is still functional, and of replacing the latter when her normal period of life expires, or she is destroyed by some fortuitous occurrence. It is not clear, however, why members of brachypterous and, more rarely, the apterous reproductive castes, should be present in such numerical strength as they are frequently met with. It seems probable that, owing to their lower fecundity, as compared with the original queen, a considerable number of such forms is necessary in order to maintain the colony up to its normal population. Once the original queen has died out it is believed that the macropterous caste can no longer be produced, and consequently colonies headed by brachypterous or apterous royalties are accounted for. Grassi and Sandias, for example, mention colonies of *Leucotermes lucifugus* in Sicily which were entirely maintained by brachypterous queens.

It will be convenient at this stage to consider the habits of the macropterous caste. So long as the original queen is in functional activity individuals of the former caste are produced. At certain times, varying with geographical location and season, the fully winged forms are brought forth in large numbers as annual occurrences. These individuals become impelled to leave the parental colony by some unknown instinct and, when the critical hour arrives, they depart on their colonizing flight and are said to be "swarming." Atmospheric conditions are an important factor influencing the actual time of issue: thus, in the more arid regions, the flight takes place during the rainy season, or after casual showers, when the moisture content of the atmosphere is favourable. Prior to the flight, the workers make exit holes when necessary in the walls of the termitarium, and numerous members of this caste, along with soldiers, congregate around and often just outside these apertures while swarming is in progress. The latter may be either diurnal or nocturnal according to the species, those that swarm by night being strongly attracted to lights. Termites are weak fliers and, unless aided by the wind, these swarms do not travel any great distance. They have for their object the perpetuation and further diffusion of the species which is enabled, in this manner, to found new colonies away from the immediate proximity of the old. As a rule a number of colonies of a species swarm about the same time: the members of a swarm comprise individuals of both sexes which may either pair with each other or intercross with those of neighbouring swarms. Notwithstanding the vast numbers of termites composing these swarms, enormous mortality occurs during and after the flight, very few individuals surviving to fulfil their destiny : birds, lizards and small mammals devour the greater number. The survivors sooner or later alight or fall on the ground and cast their wings. The loss of these organs is clearly an advantage to the race, since they have served their function and their retention would prove a useless encumbrance. The sexes segregate into pairs and after an interval of courtship mating takes place. The latter may occur either before (Fuller, 1915) or after deälation : in *Leucotermes flavipes* it is not fulfilled, according to Snyder, until about one week after swarming. Both sexes participate in the early operations of forming a habitation which consist in the excavation of a small burrow or gallery, termed the nuptial chamber. The first-laid eggs are few in number, and are tended by the young parent royalties. Most of the early broods develop into workers, the latter caste being the most necessary for the building up of the incipient colony. In *Leucotermes lucifugus* Feytaud states that the first workers become functional about seven months after the swarming, and that no soldiers are present in the initial broods. The newly hatched nymphs are fed by their parents on prepared food and the wood-feeding species, for example, do not resort to a ligneous diet until later in their development. As the growth of the colony proceeds, and more eggs are produced, the duty of tending the brood is assumed by the workers, who also enlarge the habitation and generally make provision for the growing community. During the first season members of the reproductive castes are usually not produced. The queen gradually grows in size, and is subjected to constant care and feeding by the workers. She no longer partakes of her original ligneous or other food, but receives a prepared diet from the workers : mastication becomes no longer necessary and the jaw muscles degenerate. With her increase in size, there is a corresponding increase in the number of eggs produced. In established colonies of the higher termites the queens are capable of laying some millions of eggs apiece during their lifetime. Thus Fuller observed that a queen of *Termes badius* is capable of laying 4,000 eggs in 24 hours. From a dissection of a queen of *T. redemanni* Bugnion estimated that the two ovaries contained 48,000 eggs at the time of examination. Under more or less uniform tropical conditions a single queen is probably capable of producing, at her period of maximum fecundity, at least a million eggs in the year. Much higher estimates are given by some authorities but the figures need confirmation. The duration of life for the queen is extremely difficult to estimate, but probably six to nine years is an approximately accurate statement.

The food of termites consists primarily of wood and other vegetable tissue. These insects also consume proctodæal matter ejected by their fellows and, by this means, the younger nymphs of the wood-feeding species first become infected with Protozoa derived from the fæces of the older members of the community. Exuviæ and the bodies of dead termites are also devoured. The nymphs at first only receive saliva ; later on they are fed with stomodæal or proctodæal food until they are able to eat the staple vegetable diet.

The habit of foraging outside the nest occurs among various species of Termitidæ, and it is also found in *Hodotermes* among the Calotermitidæ. The workers and soldiers of species of this genus possess well developed compound eyes, and exhibit the unusual habit of foraging above ground during daylight. Sorties are made from the nest for the purpose of collecting grass, pine needles, etc., which are cut into short lengths, and carried to the mouth of the burrow. Here the material is either taken directly within, or allowed to accumulate to form a mound whose contents are subsequently removed into the nest. Among certain Termitidæ the foraging habits of *Termes latericus* and *Eutermes trinervius* in S. Africa are described by Fuller (1915). In the former species there are special cells or granaries within the nest, and lengths of green grass, together with large quantities of seeds are collected. *E. triodiæ*, in Australia, stores dried grass in chambers which are situated in the walls of the termitarium from the ground to the summit. Bugnion (1914) describes the habits of the " black termite " (*E. monoceros*) of Ceylon. Long dense files of workers of this species set out about sunset, with the soldiers aligned up on guard on either side of the procession. The object of these expeditions is to gather fragments of lichens which serve to nourish the young. Having found a suitable tree, they remain the whole night gathering provender, and return the following morning. Bugnion calculated, by means of photographs, that there are, on an average, 1,000 termites to each metre of the moving column and, if the army marched out for five hours, moving at the rate of a metre per minute, about 300,000 termites would be involved in the procession.

The habitations of many of the higher termites, particularly species of the genus *Termes* and its allies, contain what are commonly termed " fungus gardens." These beds are composed of a spongy dark reddish-brown coral-like " comb " which is constructed by the workers of comminuted vegetable matter forming the excreta (Figs. 293–295). The chambers containing the fungus gardens are located near the centre of the nest, often in close proximity to the royal cell, or in communication with the latter. Fungal hyphæ grow upon the substratum formed by the comb and produce small white " spheres " which form the nutriment of the royal pair and young nymphs. The fungal chambers also serve as nurseries for the eggs and young brood ; Bugnion (1914) states that in species observed by him in Ceylon the young nymphs may be observed grazing on the fungus beds after the manner of miniature sheep !

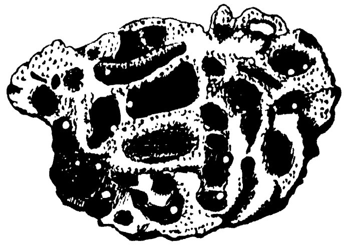

FIG. 295.—FUNGUS BED OF *ODONTOTERMES*, INDIA : THE SMALL WHITE FUNGAL SPHERES ARE SEEN GROWING ON THE SUBSTRATUM. × 2.

According to Petch the " spheres " produced by the fungi are composed of branching hyphæ bearing either spherical or oval cells. The oval cells germinate readily, but it has not been possible to reproduce the original " spheres " from them. On a normal comb just removed from the nest the only fungi evident are the " spheres " and their mycelia. If the comb be placed beneath a bell-jar a *Xylaria* regularly grows from it in about two days : it also grows from deserted combs after rain. When the combs are getting old, and falling out of use, an agaracine fungus develops upon them : various names have been assigned to it and it is regarded by Petch as a species of *Volvaria*. It has not been possible to germinate the spores of the latter or prove experimentally that the " spheres " are a phase in the growth of the *Volvaria*. Other fungi also develop upon the comb when the latter is removed from the influence of the termites, and it is believed that these insects weed out such extraneous fungi when they appear in the nest. There is a considerable literature on the fungus-growing habits of termites and the reader is referred to the works of Petch (1906) and Escherich (1909) for more detailed information.

In addition to the normal occupants of a termite habitation, there is also a very extensive termitophilous fauna consisting of various insects, and other arthropods, which are represented in almost every community by one or more species. The relations between these guests and their hosts are, so far as is known, very similar to those described later on between myrmecophilous species and ants. The termitophilous forms similarly include true guests or symphiles, indifferently tolerated guests or synœketes, and synechthrans which are scavengers or predators. The largest number of termitophilous insects belong to the Coleoptera. The Carabidæ are principally represented by the larvæ of *Orthogonius*: the Staphylinidæ include such genera as *Corotoca*, *Spirachtha*, *Termitobia*, *Termitomimus*, *Doryloxenus*, etc., while the Pselaphidæ, Scarabæidæ, Tenebrionidæ and other families have sundry representatives. Among the Diptera are certain remarkable Phoridæ including *Termitoxenia*, *Termitomyia* and *Ptochomyia*: included in this same order are the equally remarkable Psychodid *Termitomastus*, and several genera of larval Anthomyidæ. The Thysanura include a large number of termitophilous forms, there are also a few Collembola of similar habits, several larval Tineids and, among the Hemiptera, the anomalous genus *Termitaphis*. In addition to insects the list includes Acarina, Diplopoda and Chilopoda. The literature on termitophilous arthropods is extensive and is principally comprised in numerous papers by Wasmann (1894 onwards) and Silvestri (1903, 1905, 1914–1920). Termite mounds also afford shelter to lizards, snakes and scorpions, while certain birds are even known to nest in them.

It is noteworthy that more than one species of termite may inhabit the same habitation and that a kind of social symbiosis exists in consequence. Thus *Anoplotermes*, which has no soldiers, is usually associated with species of other genera. In S. America five species of termites, belonging to as many different genera, are recorded by Holmgren as sharing a habitation of *Termes dirus*, while no less than eight different species are mentioned by Escherich as living amicably with *Termes chaquimayensis*. Certain members of the genus *Eutermes* particularly exhibit this habit of guest species. Termites and ants have often been recorded as inhabiting the same log, or other object, where they may occupy contiguous galleries or even intermingle. Under ordinary circumstances the relations between the two kinds of insects are friendly, unless the nest be disturbed, when the ants soon attack and carry off the termites.

Origin of Polymorphism

The origin of caste in termites has been productive of much discussion, while the problem as to how the characters of the sterile soldiers and workers secure representation in the germ cells of the species has been an outstanding difficulty to students of heredity. The theories which attempt to account for the origin of caste in these insects may be briefly summarized under two headings, viz. theories of extrinsic and intrinsic causes.

1. **The Theory of Extrinsic Causes.**—The principal upholders of this theory are Grassi and Sandias (1897). These observers believe that nutrition and method of feeding are of paramount importance. In the termites studied by them the newly hatched nymphs are externally alike but, when they attain a length of 2 mm. or over, they become separable into large and small headed forms. The large-headed forms develop into

soldiers and, in *Leucotermes*, into workers also: the small headed forms develop into the macropterous caste or, as in *Calotermes*, the head may increase in size and such individuals develop into workers. Grassi and Sandias conclude that the development into soldiers and workers, on the one hand, and into macropterous forms on the other, is due to the relative amounts of salivary food received from the nymphs which feed them during the early phase of development. Young destined to produce macropterous forms continue to be fed with saliva for a much longer period than those which will ultimately develop into soldiers and workers. Grassi and Sandias maintain that the early appearance of intestinal Protozoa, and their constant presence in great abundance in the two latter castes, are associated with the smaller amount of saliva received. It is also implied by them that the Protozoa exercise an inhibitory effect upon the development of the gonads. They further maintain that, by means of selective feeding, nymphs already far advanced towards becoming macropterous adults can be diverted, as it were, and develop into soldiers. Others may be converted into neoteinic forms and thus assume a precocious sexual maturity.

Among other biologists Silvestri (1902, 1903) maintains that food is the determining factor in caste production but acts indirectly since the germ plasm is also involved. Desneux (1904) believes that the cause of the differentiation of the young nymphs is the particular diet which they receive. Escherich (1909) believes that food is of paramount importance in caste differentiation but he assumes, with Weismann, that it does not exert a direct influence but provides the stimulus which releases, as it were, the potentialities of the different castes, these potentialities being present in the egg cells. Holmgren (1909) seeks to explain polymorphism on the basis of his exudation theory. According to him the newly hatched nymphs are alike in appearance but from the commencement some may receive a little more food and produce rather more exudation than others. These latter nymphs are consequently more frequently licked and attended by the workers and finally develop into sexual forms. Those nymphs which produce less exudation, and receive at first less food, are subjected to less care from the workers and develop into the sterile castes. Holmgren's theory, however, has received little support and the existence of exudatory tissue has no direct influence on caste production.

Intestinal Protozoa and their Significance. Living within the hind-intestine of many termites is an abundant Protozoan fauna. If a small drop of the brown turbid contents of the gut be examined by the microscope, it is seen to be composed almost entirely of vast numbers of Protozoa, actively traversing the field of vision in all directions. They consist principally of Flagellates, belonging more especially to the peculiar order Hypermastigina (Trichonymphidea), which is almost exclusively confined to the Isoptera. These Protozoa were first observed in termites by Lespes in 1856, and since that time many genera and species have been discovered (vide Imms, 1919). The inter-relationships of these organisms with their hosts have given rise to much discussion. Several authorities regard them as being parasites; thus Grassi and Sandias, in their studies on Italian termites, maintain that the relative abundance of the Protozoa is in inverse proportion to the degree of development of the gonads of the hosts. According to these observers Protozoa abound in the hind-gut of the soldiers and workers (with aborted gonads), but are rare or totally absent in the reproductive castes. According to Brunelli (1905) in queens of *Calotermes flavicollis* and *Leucotermes lucifugus*, infested with Protozoa, there is a correlated destruction of the oocytes—a kind of indirect " castration parasitaire ": this conclusion, however, is disputed by Feytaud (1912). The researches of Bugnion, the present writer and others do not support the views of Grassi and Sandias. It is found that the presence of Protozoa is correlated with a ligneous diet on the part of their hosts. The former do not occur in the young nymphs, kings or queens which are fed with a special diet provided by the workers or older nymphs. In the soldiers and worker-like forms of *Archotermopsis* which possess fully developed gonads, a rich Protozoan fauna is always present in the hind-intestine. Feytaud also mentions having found abundant Protozoa in the macropterous caste of *L. lucifugus* nearing sexual maturity, and they are also frequent in the same caste of *Archotermopsis.* There does not appear, therefore, to be any correlation between the presence of Protozoa and the condition of the sexual organs. Buscalioni and Comes (1910) regard the Protozoa as being symbionts rather than parasites. By their action in breaking down ligneous matter the Protozoa provide nutritive material capable of absorption by their hosts. Certain species, however (those of *Dinenympha* for example), attach themselves to the walls of the intestine and are probably parasitic. The symbiotic theory has received strong support from the recent experimental observations by Cleveland (1924–28), who showed that termites are incapable of digesting cellulose without the intervention of Protozoa (vide also p. 112). It is further evident that species of termites which feed on wood harbour these microörganisms in their digestive canal. Most of the higher termites, forming the family Termitidæ, appear to be devoid of Protozoa and, in many cases, they feed upon fungi or humus. The Protozoan fauna of termites has been investigated from the cytological standpoint by many workers. The most recent study is by Sutherland (*Quart. Journ. Micros. Sci.* 76, 1933) and references to the literature on the subject will be found in this paper.

The Theory of Intrinsic Causes.—Bugnion (1912A and 1913) appears to be the first modern observer to bring forward evidence suggesting that caste differentiation occurs during embryonic life and is independent of the effects of any dietary régime. He ascertained that the nasute soldier of *Eutermes lacustris* is already clearly separable from nymphs of other castes at the time it issues from the egg, the distinguishing features being the presence of a frontal process and a relatively large frontal gland Thompson (1917) found that in *Leucotermes flavipes,* and (1919) in a number of other termites the newly hatched young, although externally all alike, are differentiated by internal characters into two types. (*a*) Reproductive castes with large brain, large sexual organs and usually a dense opaque body: and (*b*) sterile castes with small brain, small sexual organs and usually a clear transparent body. In *L. flavipes* the nymphs of the reproductive castes, on attaining a length of 1·3–1·4 mm. become further differentiated into two kinds which eventually give rise to the macropterous and brachypterous forms respectively. The ontogeny of nymphs which develop into the apterous reproductive caste has not been followed. The nymphs of the sterile castes become separable into future soldiers and workers at a later stage in their ontogeny, i.e.: when the body-length reaches 3·75 mm.

In the light of the foregoing remarks there is no conclusive evidence that any particular kind of nutrition, or the absence thereof, is capable of producing such fundamental changes as are involved in caste differentiation. It has also been mentioned on an earlier page that an abortive condition of the sexual organs is not an invariable attribute of the soldier and that caste production is not in any way related to the presence of intestinal Protozoa. It is evident also that too much stress has been laid on the *apparent* similarity of the young of almost all termites when newly emerged from the egg. This fact has given rise to the belief that caste differentiation takes place during post-embryonic growth when its presence first becomes obvious. It is necessary, therefore, to look to some intrinsic cause or causes to account for the phenomenon. In seeking to explain polymorphism by means of intrinsic factors the question arises as to whether the cytology and development of the germ cells would yield important evidence but, up to the present, this field remains unexplored. The phylogenetic origin of termite castes appears to be explainable on the basis of the mutation theory, i.e. : that the castes are secondary and have arisen as inheritable variations of some stage in the ontogeny of the macropterous form, or original winged imago (vide Imms, 1919, Thompson and Snyder, 1919, Snyder, 1920). It is possible that the beginning of polymorphism in termites was the occurrence of dimorphic males and females —one form being apterous and the other being represented by ordinary macropterous individuals. Later in evolution the apterous forms tended towards increased head development and they ultimately became differentiated into soldiers and workers. These apterous individuals gradually lost their capacity to reproduce, degeneration of the sexual organs resulted and the secondary sexual characters likewise gradually atrophied. This combined process went on until, in the higher termites, all external indications of sex became lost. Once the individuals of a caste became sterile their racial persistence, on this theory, would not necessarily cease. If it be assumed that the fertile individuals are heterozygous for caste, both soldiers and workers will appear in each successive generation by the recombination of the respective genes that are involved.

At the present time there is very little exact information available with regard to the constitution of the progeny of the three reproductive castes. So far as is known the queens of the macropterous form are the parents of all the remaining castes. According to Snyder (1920), both field observations and breeding experiments seem to indicate that the brachypterous and possibly the apterous forms produce, in addition to soldiers and workers, their own fertile types and never the macropterous form.

The theory of intrinsic causes has been called into question by Jucci (1924) and by Heath (1927). In *Termopsis* Heath was unable to discover any external evidences of caste differentiation either among newly hatched individuals or in any growth stages up to a late instar. Jucci's experiments are concerned with the influence of nutrition on caste production and he supports the theory that it is of paramount importance in this respect. In the present state of knowledge the evidence for both the extrinsic and intrinsic theories is still very inconclusive and there is an evident need for crucial experimental tests.

Metamorphosis

It has been pointed out that the newly hatched nymphs, although apparently all alike, are already differentiated by internal characters into productive and worker-soldier types. At a later stage in development they become separable into their individual castes. In the case of the workers there is very little external change of any description during postembryonic growth, and they are consequently ametabolous. In both the mandibulate and nasute castes of soldiers metamorphosis is indicated by very considerable external and internal changes, which more particularly affect the head and mandibles. The macropterous reproductive caste exhibits the usual hemimetabolous growth which is also present, although to a much lesser degree, in the brachypterous caste. The apterous reproductive caste passes through no changes sufficiently marked to be regarded as metamorphosis.

Development is slow, particularly in the reproductive members of the community whose period of growth may occupy two years (Snyder). According to Heath (1927), in *Termopsis*, the soldiers become adult from the fifth or sixth instar, but in old colonies this condition becomes progressively delayed and may not be attained until the ninth instar. The winged adults, on the other hand, are invariably in the eighth instar. Prior to the last ecdysis, anal styli are present in both sexes, irrespective of their caste, but after the final moult these organs are usually lost in the females of the reproductive forms.

In their development termites pass through resting or quiescent phases during ecdysis (Snyder, 1913). These phases are to be regarded as prolongations of the periods of inactivity which accompany each ordinary moult. Such a resting condition is most evident (1) during the ecdysis when apparently undifferentiated nymphs transform into those of the soldier type and (2) during the final ecdysis which is followed by the adult instar. The quiescent condition is more strongly pronounced in some genera than others and, where this phase is very much in evidence, the insect lies upon its side, with the head flexed upon the ventral aspect of the thorax, while the limbs and other parts remain immobile. The transition between an insect in this condition during its final ecdysis, and a pupa of the Neuroptera, for example, is a comparatively slight one, and the differences are mainly those of degree. The quiescent phase in termites evidently fulfils the same functions as a pupa, since all the more important changes, both external and internal, occur while it lasts. Its duration varies from a few hours up to several days, the shorter period being prevalent in cases where the resting phase is only slightly pronounced. The ontogeny of termites, therefore, affords to some extent a connecting link between the hemimetabolous and holometabolous types of development.

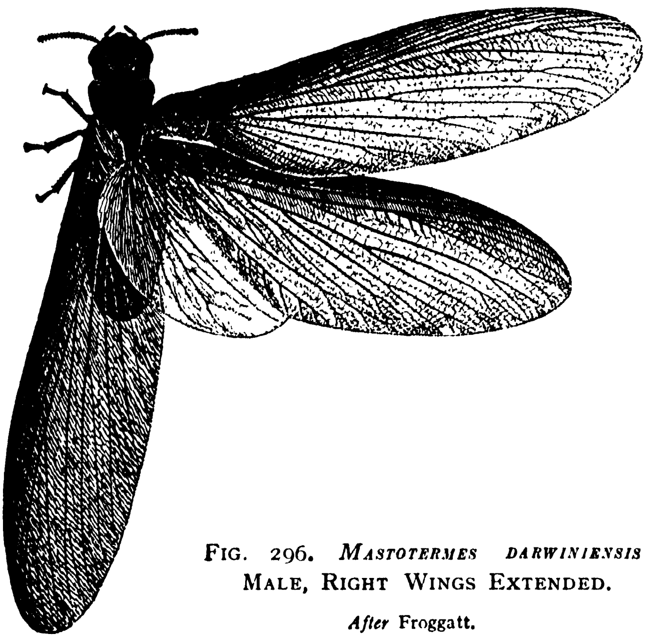

Fig. 296. *Mastotermes darwiniensis* Male, Right Wings Extended.

After Froggatt.

Classification

Among recent systems of classification those of Desneux (1904) Silvestri (1909) and Holmgren (1911) are notable. That of the first mentioned authority comprises three sub-families—the Mastotermitinæ, Calotermitinæ and Termitinæ which together constitute the single family Termitidæ. In the classification of Silvestri the Mastotermitinæ are elevated to family rank while Desneux' second and third sub-families are united to form the family Termitidæ. Banks and Snyder divide the termites into three families as enumerated below. For a general textbook on the order vide Hegh (1922).

A. Tarsi 5-jointed in all castes: hind-wings with a well developed anal lobe.

FAM. I. MASTOTERMITIDÆ.—Includes the single genus *Mastotermes* from northern Australia (Fig. 296).

B. Tarsi 4-jointed, or rarely imperfectly 5-jointed, in all castes; hind-wings without an anal lobe.

FAM. II. CALOTERMITIDÆ.—FONTANELLE ABSENT IN ALL CASTES. CLYPEUS WITHOUT MEDIAN LINE. RADIUS BRANCHED. SOLDIERS USUALLY WITH COMPOUND EYES AND THE MANDIBLES WITH A DENTATE INNER BORDER. Representative genera: *Archotermopsis* (Desn.), *Termopsis* Heer, *Hodotermopsis* Holmg., *Hodotermes* Hag., *Calotermes* Hag.

FAM. III. TERMITIDÆ.—FONTANELLE PRESENT IN ALL CASTES. CLYPEUS WITH MEDIAN LINE. RADIUS UNBRANCHED. SOLDIERS ALMOST ALWAYS DEVOID OF COMPOUND EYES AND THE MANDIBLES RARELY DENTATE ALONG INNER BORDER. Representative genera: *Leucotermes* Silv. (including *Reticulotermes*), *Psammotermes* Desn., *Coptotermes* Wasm., *Termitogeton* (Desn.), *Rhinotermes* Hag., *Serritermes* Wasm., *Acanthotermes* Sjost., *Termes* (L.) Holmg., *Odontotermes* Holmg., *Microtermes* Wasm., *Armitermes* Wasm., *Eutermes* Mull., *Anoplotermes* Mull., *Hamitermes* Silv., *Mirotermes* (Silv.), *Capritermes* Wasm.

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Order 8. EMBIOPTERA

SOLITARY OR GREGARIOUS INSECTS LIVING IN SILKEN TUNNELS. MOUTHPARTS ADAPTED FOR BITING, LIGULA 4-LOBED. TARSI 3-JOINTED; 1st JOINT OF ANTERIOR PAIR GREATLY INFLATED. BOTH PAIRS OF WINGS ALIKE: VEINS BUT LITTLE PRONOUNCED, R GREATLY THICKENED, REMAINING VEINS OFTEN REDUCED OR VESTIGIAL. CERCI 2-JOINTED, GENERALLY ASYMMETRICAL IN THE MALE. FEMALES APTEROUS AND LARVIFORM. METAMORPHOSIS GRADUAL IN THE MALE, ABSENT IN THE FEMALE.

The Embioptera are a small group of fragile insects with a soft thin cuticle and weak powers of flight. All are sombre coloured, being either brown or yellowish brown, with smoky wings. In their habits these insects generally avoid daylight, living beneath stones, or under bark, etc. The females are much more rarely met with than males, the latter not infrequently being attracted to a light. Sexual dimorphism is a marked characteristic of the order, the males being winged and the females apterous (Figs. 297, 298). In several species, notably *Embia texana* (Melander, 1903), both winged and wingless males are present.

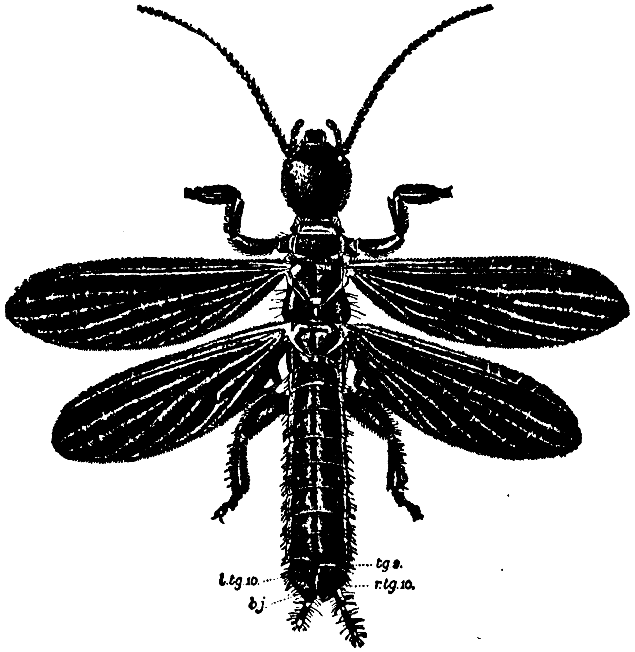
tg. 9.
l.tg. 10.
r.tg. 10.
bj

FIG. 297. *EMBIA MAJOR*, MALE. INDIA.
*Tg*9, 9th tergum; *tg*10, right and left plates of 10th tergum; *bj*, basal joint of left cercus. From Imms, 1913.

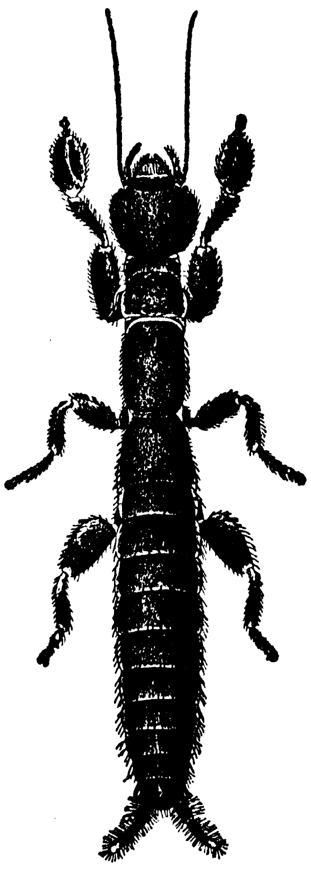

FIG. 298. *EMBIA MAJOR*, FEMALE.
From Imms, 1913.

The most striking feature in the biology of the Embioptera is their habit of constructing silken tunnels in which they live (vide Imms, 1913). When disturbed in these retreats they are able to run backwards or forwards with equal agility. *Embia major* is gregarious and upwards of twenty individuals may be found associated together. This species constructs a nest composed of a series of superimposed silken tunnels communicating usually with one or two subterranean chambers (Fig. 299). In addition to forming a retreat, it is probable that these tunnels subserve other functions—they appear to be adapted for protection against predaceous insects which would become entangled in the threads should they attempt to enter them. Grassi and Sandias consider that they serve to protect the body from an excessive loss of moisture and to retain about the occupants an atmosphere not too dry. During the construction of the tunnels the fore-legs are in constant activity, crossing and recrossing one another repeatedly. The faculty of weaving the tunnels is possessed equally by both sexes and also by the nymphs. Newly hatched nymphs, when removed from the proximity of the parent female, were observed to weave fine tunnels on their own account. The method of production of the silk has given rise to discussion. On the plantar surface of the 1st and 2nd tarsal joints of the fore-legs are a number of hollow bristles which communicate, each by means of a fine duct, with a small glandular chamber. The chambers are situated on the lower area of the enlarged 1st tarsal joint; each is bounded by a single layer of epithelium which encloses a central space filled with a viscid secretion (Fig. 300). In *Embia texana* Melander estimates that about 75–80 chambers are present in the whole joint. Since a fine thread is emitted from each bristle a number are available simultaneously, which accounts for the rapidity with which these insects weave their tunnels (Melander, 1903: Rimsky-Korsakow, 1905). Enderlein (1912), however, disputes this explanation of silk production and maintains that the glossæ function as a spinneret which receives the ducts of spinning glands.

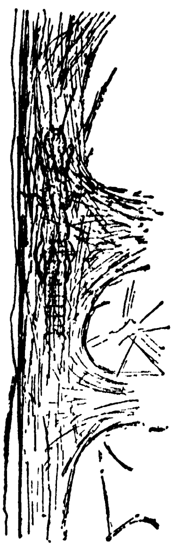

FIG. 299. *EMBIA TEXANA*, FEMALE IN SILKEN TUNNEL.

After Melander, *Biol. Bull.*, 1902.

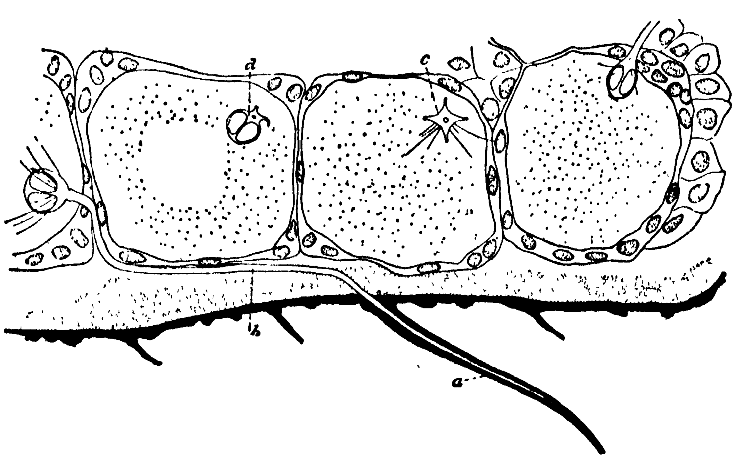

FIG. 300. *EMBIA TEXANA*, SECTION OF PORTION OF 1ST TARSAL JOINT, SHOWING SILK GLANDS.

a, spinning bristle; *b*, duct of silk gland; *c*, *d*, ampullæ at bases of ducts. *After* Melander *Biol. Bull.*, 1902.

Very little information exists with reference to the feeding habits of these insects. Both sexes of *Embia* have been reared from the egg upon vegetable food, but it is likely that the males are normally more or less carnivorous, and their mandibles differ markedly in form from those of the opposite sex.

The eggs are elongate-cylindrical with a conspicuous operculum at one pole. They are laid in small groups along the course of the silken tunnels of the nests, and the females exhibit parental care for their offspring after the manner so well known in Dermaptera.

Embioptera are tropicopolitan but extend their range into the warmer temperate zones. They occur in all zoo-geographical regions including Australia, and species are also found in Madagascar, New Zealand, Ceylon and various smaller islands. Three species, comprised in as many genera, are European and are found in countries bordering on the southern littoral of that continent. It is noteworthy that *Oligotoma Michæli* MacLach. has been found in a London orchid house where it had become temporarily established. *O. Saundersi* Westw. is stated to be so abundant on Ascension I. as to become injurious.

External Anatomy.—The head in the Embioptera is always rather small and projects in a line with the body: the epicranial suture is wanting and there are no ocelli. The compound eyes are reniform in the males and rather smaller in the females. The antennæ are filiform, shorter than the body, and composed of 15–32 joints.

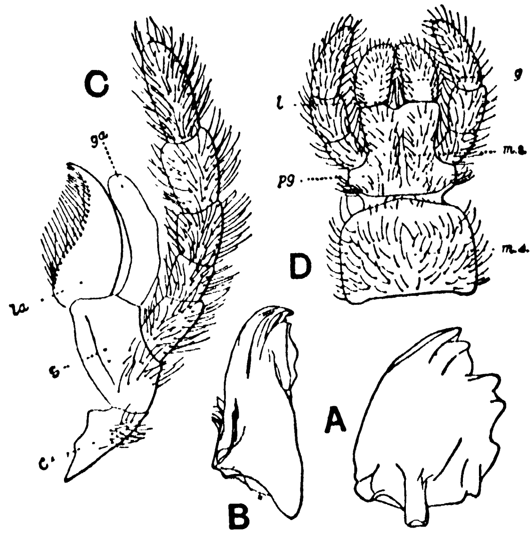

FIG. 301. *EMBIA MAJOR.*

A, left mandible of female. B, do. of male. C, right maxilla, *c*, cardo; *s*, stipes; *la*, lacinia; *ga*, galea. D, labium (ventral), *g*, paraglossa; *l*, glossa; *pg*, palpiger; *m1*, prementum; *m2*, postmentum.

The mouth-parts (Fig. 301) are typically Orthopteran in character: both the labrum and clypeus are well developed, and the mandibles differ considerably in the two sexes. Those of the male are much more slender and have fewer teeth than in the female. The maxillary palpi are 5-jointed, the galea is membranous and the lacinia chitinized and provided with a pair of apical teeth. Both cardines and stipites are well developed. In the labium the ligula consists of a pair of rather fleshy paraglossæ and, between the latter, lie the very small pointed glossæ: the labial palpi are 3-jointed. The hypopharynx is large and its dorsal surface is covered with minute pectinate scales.

The prothorax is narrower than the head, and a deep transverse sulcus cuts off the anterior portion of the pronotum from the remainder. The meso- and meta-thorax are sub-equal in size and broader than long in the male, but elongate and narrower in the female. The fore-legs are stout, the middle pair are reduced in size, and the hind pair resemble those of leaping insects owing to their swollen femora. The tarsi are always three jointed: the first joint of the anterior pair is inflated at all stages of life and in both sexes.

The two pairs of wings (Fig. 302) are almost identical in size and shape and only differ in unimportant details with regard to the venation—a similarity which finds a parallel among the Isoptera. The wing membrane is smoky in colour, with narrow hyaline areas running in a longitudinal manner between the principal veins, giving the wings a very characteristic appearance. After the last ecdysis the newly expanded wings are clear and subsequently assume the fuscous coloration, the hyaline areas remaining unmodified. The surface of the wings is clothed with microtrichia, together with macrotrichia distributed along and between the veins. The radial vein is always greatly thickened, thus serving to strengthen the anterior portion of the wing; the remaining veins are for the most part weakly defined, exhibiting reduction and degeneration (Fig. 302). The venation is seen in its most generalized condition in *Donaconethis*, but even in this genus reduction is evident, as R_s is only 3-branched and M is represented by a single fork. In the Oligotomidæ the venation is greatly reduced and markedly degenerate: R_{4+5} is represented by a mere spur, M has practically disappeared and Cu is unbranched. Traces of a former more complete venation are evident as slight thickenings of the wing membrane.

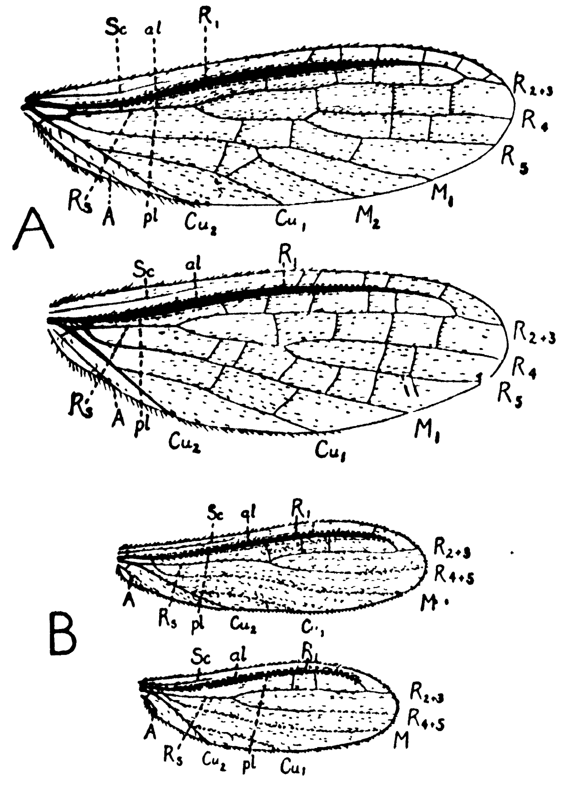

FIG. 302. RIGHT WINGS OF A, *EMBIA MAJOR*; B, *OLIGOTOMA LATREILLEI*.

al, *pl*, anterior and posterior radial lines.

The abdomen is composed of 10 evident terga: in the females, and the immature forms of both sexes, the 10th tergum is entire but in the adult males it is divided into a pair of asymmetrical plates. One or both of these plates is drawn out into a horny process of variable form. In *Clothoda* (S. America) the 10th tergum of the male is entire and symmetrical as in the female. A pair of 2-jointed cerci are present at the apex of the abdomen and, as a general rule, the left cercus in the male is modified basally and the pair is asymmetrical in consequence. In *Clothoda*, however, the cerci are unmodified, and these organs exhibit also only slight asymmetry in the Oligotomidæ. Each cercus is borne upon a basal plate, and these plates are universally present in the females and immature forms of both sexes. Among the males they have disappeared in certain of the more specialized forms. Morphologically they are probably to be regarded as vestiges of an 11th segment. Ten sterna are present, although this number is not always evident and, in the Oligotomidæ, the 1st sternum in the female is largely aborted. In the immature forms of both sexes, and the females, the 10th sternum is divided into two symmetrical plates. In the males the 9th sternum is a composite plate apparently formed by the fusion of the 9th and 10th sterna, and is usually asymmetrical in form. The female genital aperture is placed on the hind border of the 8th sternum, the latter functioning as the subgenital plate. In the male the composite 9th sternum is the subgenital plate.

Internal Anatomy.—The internal organization of the Embioptera needs fuller investigation as its general features are mainly known from fragmentary accounts by Grassi and Sandias (1897–98) and Melander (1903). It is evident, however, from the descriptions of these observers that it is a generalized type. The *alimentary canal* is an almost straight tube from the mouth to the anus. The mouth leads into a small buccal cavity which is lined with backwardly directed denticles. This is succeeded by a narrow pharynx, and the remainder of the fore-intestine consists of a large dilated œsophagus and crop. The mid-intestine is a long tubular chamber which narrows somewhat posteriorly. The hind-intestine consists of a slightly coiled ileum, a very short colon and a dilated rectum, the latter being provided with six cushion-like rectal papillæ. *Malpighian tubes* are variable in number: in adult individuals there are about 20–24 of these organs. A pair of large *salivary glands* and reservoirs are present in the thorax, and their ducts unite anteriorly to form a common canal which opens on the floor of the mouth. The *nervous system* consists of a rather small supra-œsophageal ganglion, a sub-œsophageal ganglion, and a chain of three thoracic and seven abdominal ganglia, which are united throughout by double connectives: the visceral system is also well developed. The *tracheal system* communicates with the exterior by means of ten pairs of spiracles which belong to the meso- and meta-thorax, and first eight abdominal segments respectively. The tracheæ anastomose by longitudinal and transverse branches. The *reproductive organs* exhibit indications of a primitive segmental arrangement recalling that found in certain of the Thysanura. Each ovary consists of five (panoistic ?) ovarioles which open at intervals along the course of the oviduct: there is a short vagina which receives the aperture of a large spermatheca. There are similarly five testes on either side, which are disposed successively along the course of the vas deferens. The latter tube dilates posteriorly to form a vesicula seminalis and ultimately unites with its fellow to form a common ejaculatory duct: two pairs of accessory glands are also present.

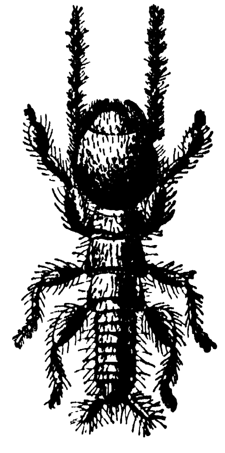

FIG. 303. *EMBIA MAJOR*, NEWLY-HATCHED NYMPH. From Imms, 1913.

Post-embryonic Growth (Fig. 303).—Metamorphosis is wanting in the females and comparatively slight in the case of the males. The newly hatched young of both sexes do not differ in any important characters from the female parent and, in individuals of the latter sex, the whole postembryonic development is one of simple growth, unaccompanied by structural change. In the males, the nymphs do not differ from the newly hatched young until the appearance of the wing-buds, when the thorax also undergoes correlated changes. The characteristic asymmetry of the terminal abdominal segments is only assumed with the final ecdysis.

Classification.—About 60 species of Embioptera have been described and of these about 42 have been based upon an acquaintance with one sex only, almost always the male. Among recent authorities both Krauss (1911) and Enderlein (1912) have monographed the order but these two writers differ radically with regard to classification and synonomy. The system of Enderlein is followed below:

FAM. I. EMBIIDÆ.—R_{4+5} BIFURCATE, EITHER IN BOTH WINGS OR ONLY IN THE HIND PAIR. CERCI IN MALE EITHER SYMMETRICAL OR WITH THE LEFT ONE MODIFIED: 10th TERGUM ENTIRE IN BOTH SEXES OR, MORE USUALLY, DIVIDED INTO TWO ASYMMETRICAL PLATES IN THE MALE: 1st ABDOMINAL STERNUM PRESENT IN THE FEMALE. *Clothoda, Embia, Rhagadochir,* etc.

FAM. II. OLIGOTOMIDÆ.—R_{4+5} VESTIGIAL IN BOTH WINGS. CERCI IN MALE BUT LITTLE MODIFIED, ALMOST SYMMETRICAL: 10th TERGUM IN MALE DIVIDED INTO TWO PLATES WHICH ARE PRODUCED INTO A PAIR OF ASYMMETRICAL PROCESSES: 1st ABDOMINAL STERNUM VESTIGIAL IN FEMALE. *Oligotoma.*

Literature on Embioptera

DAVIS, 1936–40.–Taxonomic Notes on the Embioptera. *Proc. Linn. Soc. N.S.W.,* 61–65. **ENDERLEIN, 1912.**–Embiiden. In *Coll. Zool. du Sélys-Longchamps*: 3. **FRIEDERICHS, 1906.**–Zur Biologie der Embiiden. *Mitt. Zool. Mus. Berlin* 3. **GRASSI** and **SANDIAS, 1897–98,** vide p. 275. **IMMS, 1913.**–On *Embia major* sp. nov. from the Himalayas. *Trans. Linn. Soc. Zool.* (2) 11. **KRAUSS, 1911.**–Monographie der Embien. *Zoologica,* 32. **MELANDER, 1903.**–Notes on the Structure and Development of *Embia texana. Biol. Bull.* 4. **MUKERJI, 1927.**–On the Morphology and Bionomics of *Embia minor,* etc. *Rec. Indian Mus.* 29. **RIMSKY-KORSAKOV, 1905.**–Uber das Spinnen der Embiiden. *Zool. Anz.* 36. **VERHOEFF, 1904.**–Zur vergleich. Morph. und Systematik der Embiiden, etc. *Acta Acad. Leop. Carol. Halle,* 82.

Order 9. PSOCOPTERA (Booklice and their allies)

WINGED OR APTEROUS INSECTS OF SMALL OR MINUTE SIZE, WITH RATHER LONG 9- OR MORE JOINTED ANTENNÆ: Y-SHAPED EPICRANIAL SUTURE PRESENT: MOUTH-PARTS OF THE BITING TYPE. THORACIC SEGMENTS CLEARLY DEFINED: WINGS MEMBRANOUS, ANTERIOR PAIR THE LARGER WITH EXTENSIVE PTEROSTIGMATA. VENATION SPECIALIZED BY REDUCTION, CROSS-VEINS SELDOM PRESENT. TARSI 2- OR 3- JOINTED. CERCI VERY SHORT OR ATROPHIED: OVIPOSITOR ABSENT. METAMORPHOSIS GRADUAL OR WANTING.

The Psocoptera as defined above include the Zoraptera and Psocida which have been regarded as separate orders. The affinities of the Zoraptera are evidently near to the Psocida and, as regards the venation, closely approach that of the genus *Archipsocus* (vide Crampton, 1922).

Sub-order 1. **Zoraptera.**—INSECTS WITH MONILIFORM 9-JOINTED ANTENNÆ. MAXILLÆ NORMAL, LABIAL PALPI 3-JOINTED. WINGS, WHEN PRESENT, CAPABLE OF BEING SHED BY MEANS OF BASAL FRACTURES: PROTHORAX WELL DEVELOPED: TARSI 2-JOINTED. CERCI VERY SHORT, 1-JOINTED.

The first Zoraptera were described by Silvestri in 1913, among insects obtained from W. Africa, Ceylon and Java. More recently, Caudell has brought to light additional species from Texas, Florida and Bolivia. The known species belong to the genus *Zorotypus* which constitutes the family Zorotypidæ: they are minute insects, less than 3 mm. long, and the alate forms have a wing-expanse of about 7 mm. They occur under bark in decaying wood, humus, etc.; the two N. American representatives are generally found near the galleries of termites, but not usually living with those insects. The oriental and ethiopian species are known from apterous individuals only, but those from N. America are represented by winged and apterous forms in each instance. A third form, termed the

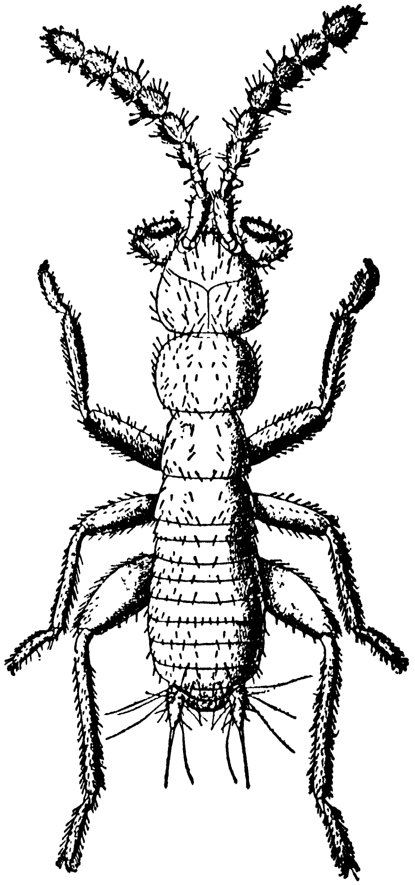

FIG. 304. *ZOROTYPUS GUINEENSIS*, AFRICA. *After* Silvestri, *Boll. Lab. Zool. Portici*, 1913.

apterous unchitinized adult, is recognized by Caudell, but it does not appear to differ from the ordinary apterous chitinized form in any morphological characters.

The mouth-parts of the Zoraptera are of a generalized type (Fig. 306). The mandibles are more or less quadrangular and adapted for mastication: the maxillæ do not call for special mention and their palpi are 5-jointed: the labium is characterized by the completely divided prementum, and 3-jointed palpi. The winged individuals possess compound eyes and ocelli, but both types of visual organs are wanting in the apterous forms. The wings are capable of being shed as in termites, but the fractures are not very definitely located, nevertheless they are situated near the bases of the veins. The wing-stumps persist in deälated individuals as in termites. The venation (Fig. 305) is greatly specialized by reduction and according to Crampton (1922) it approaches that of the Psocida. The abdomen is 10-segmented and genitalia are wanting in the female: in the male, genitalia are described by Crampton in *Z. hubbardi*. There are ten pairs of spiracles, two being thoracic and the remainder abdominal in position. The internal structure of *Z. ceylonicus* has been partially investigated by Silvestri (1913). The digestive system is characterized by the large crop which extends backwards to about the 5th abdominal segment; the stomach is an ovoid obliquely disposed sac, and the hind-intestine is convoluted. According to Silvestri there are probably six Malpighian tubes. The nervous system is highly specialized, there being three thoracic and only two abdominal ganglia, the first of the latter being located in the thorax. The testes are ovoid paired bodies communicating by slender vasa deferentia with an ejaculatory duct: the female organs are so far undescribed.

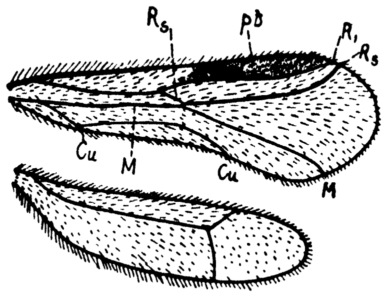

FIG. 305. *ZOROTYPUS SNYDERI*, RIGHT WINGS.

pt, pterostigma.

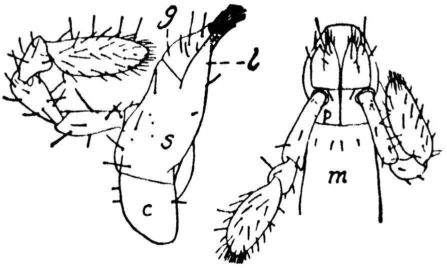

FIG. 306. *ZOROTYPUS GUINEENSIS*, MAXILLA AND LABIUM.

c, cardo; *s*, stipes; *g*, galea; *l*, lacinia; *p*, prementum; *m*, postmentum. *After* Silvestri, 1913.

From a general consideration of the structure of both winged and apterous forms, and from the fact that a colonial life is known to take place it appears possible, from the analogy of the Isoptera, that the differences in the imagines are those of caste. There is no evidence, however, relative to the occurrence of castes of sterile individuals, but at the present time next to nothing is known concerning the economy of these insects, In their affinities they appear to have relationships with the Isoptera, on the one hand, and, as already stated, with the Plecoptera and Psocida on the other.

Literature on Zoraptera

CAUDELL, 1920.–Zoraptera not an apterous Order. *Proc. Ent. Soc. Washington* 22. **CRAMPTON, 1920.**–Some anatomical details of the remarkable winged Zorapteron, *Zorotypus hubbardi* Caudell, with notes on its Relationships. *Ibid.*, 22. —— **1922.**—Evidences of Relationship indicated by the venation of the Fore-Wings of certain insects, with special reference to the Hemiptera-Homoptera. *Psyche*, 29. **SILVESTRI, 1913.**–Descrizione di un nuovo ordine di Insetti. *Boll. Lab. Zool. Portici.* 7.

Sub-order 2. **Psocida.** (**Copeognatha:** Booklice and their allies).—INSECTS WITH LONG FILIFORM ANTENNÆ, OF 13- TO ABOUT 50 JOINTS. MAXILLA SINGLE-LOBED ENSHEATHING AN ELONGATE ROD: LABIAL PALPI MUCH REDUCED. PROTHORAX GENERALLY SMALL: TARSI 2- OR 3-JOINTED. CERCI WANTING.

The Psocida are small or minute insects with rather soft, stout bodies and, in many cases, with delicate membranous wings. Individuals or generations of the winged species sometimes occur with the alary organs rudimentary; in other cases the micropterous condition appears to be an attribute of the female, and there are further species in which the possession of rudimentary wings is a constant feature in both sexes. Among the Liposcelidæ most of the species never possess any traces of wings. Several of the latter insects are familiar to the non-entomological observer and are common among accumulations of books and papers, in uninhabited and other apartments, being known as booklice or dustlice. They feed upon the paste of book-bindings, also on fragments of animal and decaying vegetable matter. Flour, meal and other cereal products are also frequently resorted to while, at times, collections of insects, and other dried natural history specimens, suffer from depredations by Psocids. These insects sometimes occur in houses in such numbers as to constitute a pest, and are usually introduced in the stuffing of mattresses, etc. They are also often abundant among straw and chaff in barns. The majority of Psocids, including the alate species, occur out of doors and are to be met with on tree-trunks, under bark, on weathered palings and walls, in birds' nests, etc., and often in situations where there are growths of lichen or moss: others are found among vegetation. They live on fragments of animal or vegetable matter, particularly on fungi and lichens: some species pass their whole lives among fungi of various kinds. Although sometimes stated to eat paper certain species feed upon moulds growing thereon and in this way reveal the injury done to the paper. Most Psocids carry foreign matter entangled among their body-hairs and in this way disseminate fungus spores. Many Psocids live gregariously and clusters of individuals, of various ages, are sometimes met with on bark, each colony being covered by a canopy of fine silken threads. The winged forms are curiously reluctant to take to flight. At times, however, they fly in considerable numbers and drift through the air after the manner of winged aphids. They have occasionally been recorded as occurring in buildings in large swarms, the commonest species concerned being *Pterodela pedicularia* L.

External Anatomy.—The head (Fig. 307) is large and very mobile, with the epicranial sutures more or less distinct. The compound eyes are markedly convex and protrude from the surface of the head: in *Troctes* they are vestigial and reduced to two small groups of ommatidia. Three ocelli are present in the winged species but these organs are wanting in the apterous forms. The *labrum* is well developed and attached to the *anteclypeus*: the *postclypeus* (prefrons of some authors) is a conspicuous sclerite often presenting an inflated appearance. The *antennæ* are long and filiform:

they are frequently 13-jointed, but the number of joints is variable and may be as high as fifty. The mouth-parts (Fig. 308) have been investigated by Burgess (1878) and Ribaga (1900). The *mandibles* are relatively large and strong, each with a broad striated molar area and a denticulated cutting edge. The *maxillæ* and *labium* are considerably modified and, in the absence of developmental evidence, the homologies of certain of their parts are largely conjectural. In the maxilla, the galea is a large fleshy 2-jointed lobe borne by a reduced stipes and there is a 4-jointed palpus. The most characteristic organ is the so-called "lacinia" (styliform appendage of Ribaga) which is represented on either side by a hard elongate rod, slightly bifurcated at its free extremity, and ensheathed by the galea. It has no articulation of any kind with the body of the maxilla, and this fact, together with certain peculiarities of its muscular connections, has led some writers to regard it as an independent structure, not homologous with any portion of a typical maxilla. Functionally, it is probably used as a kind of pick for rasping off fragments of bark and other plant-tissue. In the *labium*, the mentum is oblong, the prementum is divided and the ligula carries a pair of membranous paraglossæ. The inner lobes or glossæ are represented by a pair of minute structures forming the external conduit of the spinning glands. The labial palpi are reduced to the condition of single or, rarely, 2-jointed lobes. The *hypopharynx* is well developed and its complex structure has received diverse explanations. On the ventral aspect it bears a pair of chitinized plates—the so-called "lingual glands," but these parts appear to have no glandular structures associated with them. On its dorso-lateral aspect, the hypopharynx bears a pair of delicate lobes or *superlinguæ*. In the floor of the pharynx there is a peculiar *œsophageal sclerite* homologous with a similar structure in Mallophaga.

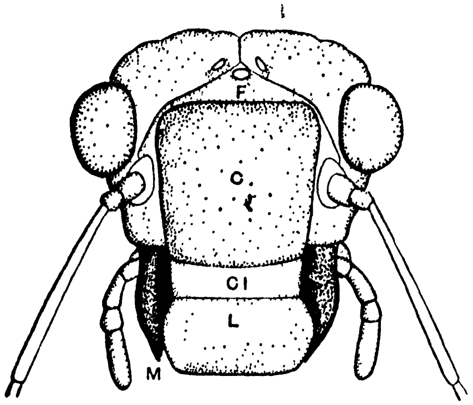

Fig. 307. Frontal View of the Head of a Psocid.

F, frons. C, post-clypeus. C1, ante-clypeus. L, labrum. M, mandible.

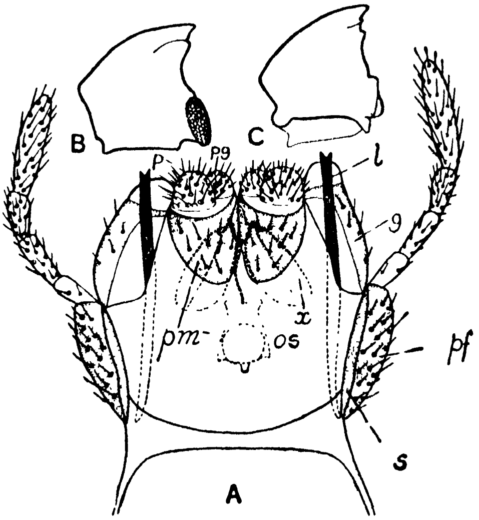

Fig. 308. A, ventral view of the head of a Psocid. B, right mandible (ventral). C, left mandible (dorsal).

g, galea; *l*, rod; *os*, œsophageal sclerite; *p*, labial palp; *pf*, palpifer; *pg*, paraglossa; *pm*, prementum; *s*, stipes; *x*, superlingua.

The *thorax* is characterized by the great reduction of the prothorax in the winged species, where it is largely concealed between the head and mesothorax. In the apterous forms the prothorax is larger, while the tergites of the meso- and meta-thorax are united into a continuous shield.

The *wings* (Fig. 309) are membranous with prominent although reduced venation: the anterior pair is considerably the larger and the wings, when not in use, are steeply inclined in a roof-like manner over the body, with the hind margins uppermost. In some species the wings are conspicuously marbled and these organs together with the body and appendages may bear scales of varied form not unlike those of Lepidoptera. The venation is discussed in detail by Enderlein (1903) and Tillyard (1923): a pterostigma is present on the fore-wing, and there is a reduction in the branches of the principal veins: Sc is unbranched, R and M are each normally 3-branched and there is a fusion of the main stems of M and Cu. In the hind-wing reduction is carried still further, M being represented as a rule by a single branch. In *Psocus*, and other genera, the wings are effectively braced on account of the somewhat tortuous courses of the veins, and there is a striking absence of cross veins. The latter exist, however, in certain members of the order.

The *abdomen* is 10-segmented but the sternum of the first segment has atrophied. There are no cerci and the male genitalia are only slightly developed and not prominent.

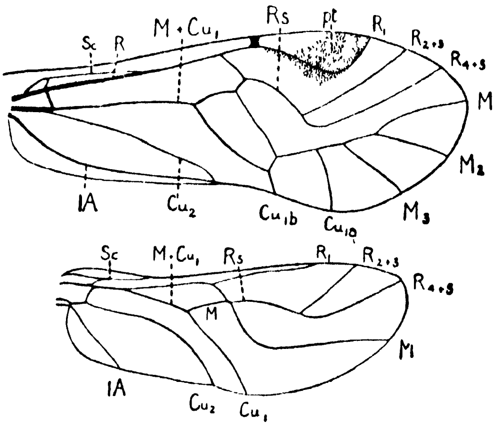

FIG. 309. RIGHT WINGS OF *Psocus bifasciatus*.
pt, pterostigma.

According to Ribaga there are three pairs of large thoracic *spiracles* and a pair on each of the first six abdominal segments.

Internal Anatomy. — Much of what is known concerning the internal anatomy of the Psocida is due to Ribaga. In the *digestive system* the œsophagus is elongate and extends into the abdomen, the stomach is sharply curved and U-shaped and leads into a very short unconvoluted hind-intestine: the Malpighian tubes are four in number. Two pairs of elongate tubular glands are described by Bertkau and by Ribaga: the former investigator also mentions a pair of spheroidal glands but their existence is not confirmed by Ribaga. Both pairs of tubular glands extend into the abdomen, and their ducts converge in the head to open along the middle line of the labium. The shorter pair of these organs are regarded by Ribaga as *spinning glands* and the longer pair, which have a somewhat different histological structure, are regarded by him as being *salivary glands.* The spinning glands provide silken threads which form the webs often associated with colonies of these insects. The *nervous system* is highly concentrated: in addition to the brain and subœsophageal ganglion there are only three other ganglionic centres. The first of these belongs to the prothorax, the meso- and meta-thoracic ganglia are fused into a common centre, and the single abdominal ganglion has shifted forwards so as to lie partly in the thorax. The connectives are extremely short but are double throughout their course. A pair of large abdominal nerves extend to the posterior extremity of the body. The *female reproductive organs* are of an extremely simple type: each ovary consists of from three to five polytrophic ovarioles, the oviducts are very short and a small globular spermatheca opens into the dorsal aspect of the vagina. A peculiar type of accessory gland was described by Nitsche in *Clothilla* many years ago: it contains from one to four small sacs each opening by a narrow canal into a common duct. The *male reproductive organs* consist of a pair of simple ovoid testes which are connected with short vasa deferentia. In *Trichopsocus* the latter open into a complex copulatory sac divided into two chambers which are enclosed in a common muscular coat. One of these chambers receives the spermatozoa while the other apparently has a secretory function of some kind. The two chambers communicate by means of a single aperture with the base of the copulatory organ. In *Clothilla* there is a pair of elongate vesiculæ seminales which are coiled in a compact manner: in the first-mentioned genus small accessory glands are also present.

Post-embryonic Growth.—The development of Psocida after eclosion from the egg has been followed by Weber (1931). The changes involved are evidently slight; in *Ectopsocus* there are six nymphal instars and, under favourable conditions, twelve generations may be passed through in a year. The eggs of some species have been observed to be laid in small groups on bark or leaves and are protected by a delicate meshwork of silken threads (Fig. 310).

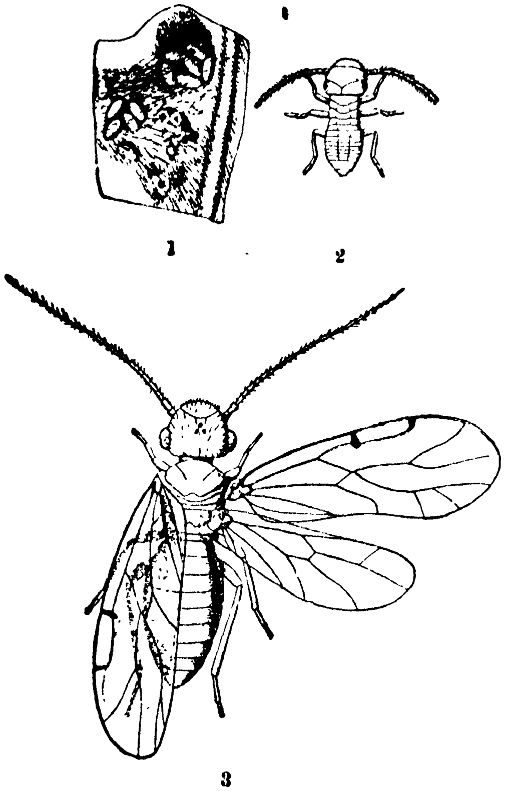

FIG. 310. *PERIPSOCUS PHÆOPTERUS.* 1, portion of leaf with eggs beneath silken threads; 2, young nymph; 3, imago.

After Silvestri.

Classification.—About 650 species of Psocida are described and of these less than fifty have been recognized in Britain. A general work on the British forms is greatly needed and little has been added to what is known concerning them since M'Lachlan's paper (1867). The order may be divided as follows, but its taxonomy needs much fuller investigation.

Superfam. I. **Trimera.**—TARSI 3-JOINTED. In *Clothilla* wing-rudiments are present on the mesothorax only while *Liposcelis* (*Troctes*) is entirely apterous. The most familiar species is *Liposcelis divinatorius*, which is common among collections of books, etc. The power of producing a ticking noise has long been attributed to this species, which has earned the name of "death watch." Sound production, however, has only been proven in the case of *Clothilla pulsatoria* and *Lepinotus inquilinus*. In the first mentioned species Pearman (1928) states that audible sounds are caused by the insect tapping a slightly thickened knob, near the apex of the ventral side of the abdomen, against the substratum upon which it is resting. The sound is most distinct when the creature is placed upon paper, more variable when it is on cardboard or wood and non-audible on glass. The sound-production appears to be confined to the female and is considered to be a mating call. In certain other Psocids the inner surface of each hind coxa bears a scale-covered swelling which, in some species, has a kind of tympanum or presumed resonator situated just behind it. It is suggested that these organs are also for sound-production and that the sound is made by the scaled swellings of the two legs being rubbed together. These organs are more largely developed in the males and the hypothesis of their sound-producing function is, at present, conjectural.

Included in this division of the Psocida are the families Liposcelidæ, Clothillidæ, Lepidopsocidæ, Mesopsocidæ, Myopsocidæ, Psoquillidæ and Amphientomidæ.

This division includes both winged and apterous forms.

Superfam. II. **Dimera.**—TARSI 2-JOINTED. Many of the common winged members of the sub-order are included in this division, which comprises the three families Cæciliidæ, Psocidæ and Thyrsophoridæ.

Literature on Psocida

BURGESS, 1878.–The Anatomy of the Head, and the Structure of the Maxilla in the Psocidæ. *Proc. Boston Soc. Nat. Hist.* 19. **ENDERLEIN, 1903.**–Die Copeognathen des Indo-Australischen Faunengebietes. *Ann. Mus. Hung.* 1. —— **1903A.**– Ueber die Morphologie, Gruppierung und systematische Stellung der Corrodentien. *Zool. Anz.* 26. **McLACHLAN, 1867.**–A monograph of the British Psocidæ. *Ent. Month. Mag.* 3. **RIBAGA, 1900.**–Osservazioni circa l'anatomia del *Trichopsocus dahlii* McLachl. *Revista Patalog. Veget.* 9. **TILLYARD, 1923.**–A Monograph of the Psocoptera or Copeognatha of New Zealand. *Trans. N.Z. Inst.* 54.

Supplementary References

ENDERLEIN, 1927.–" Flechtlinge " in Die Tierwelt Mitteleuropas, Bd. IV, Insekten, Teil 1. **NOLAND, 1924.**–The Anat. of *Troctes divinatorius* Muell. *Trans. Wisconsin Acad. Sci.* 21. **PEARMAN, 1928.**–On Sound Production in the Psocoptera and on a presumed Stridulatory Organ. *Ent. Month. Mag.* 64. —— **1928A.**–Biological Observations on British Psocoptera. *Ibid.* **WEBER, 1931.**–Die Lebens geschichte von *Ectopsocus parvulus*. *Zeits. wiss. Zool.* 138.

Order 10. ANOPLURA (Biting Lice and Sucking Lice)

SMALL FLATTENED APTEROUS INSECTS LIVING AS ECTOPARASITES OF BIRDS AND MAMMALS. ANTENNÆ SHORT, 3- TO 5-JOINTED: EYES REDUCED OR ATROPHIED, OCELLI WANTING. MOUTH-PARTS HIGHLY MODIFIED AND ADAPTED EITHER FOR BITING OR PIERCING. THORACIC SEGMENTS MORE OR LESS FUSED. LEGS SHORT, TARSI 1- OR 2-JOINTED, FEET ADAPTED FOR CLINGING TO THE HOST. ABDOMEN WITHOUT CERCI. METAMORPHOSIS WANTING.

The Anoplura live continuously in all their stages on warm-blooded animals, cementing their eggs to the hair or feathers (or clothing in man). They are divided into two naturally demarcated sub-orders—the Mallophaga and Siphunculata, the former being more especially parasites of birds while the latter are exclusively found on mammals. These two groups are commonly regarded as separate orders but the trend of modern research clearly indicates that they are sufficiently closely related to merit their union into one order. This essential fact is recognized, for example, by Harrison and by Nuttall, who adopt the name Anoplura of Leach for the order thus constituted, and revive Meinert's term Siphunculata for the Anoplura of most writers. Several authorities including Enderlein (1904) have placed the Siphunculata among the Hemiptera, mainly on account of their piercing mouth-parts. Too much stress, however, has been laid upon this one feature to the exclusion of other characters. The Mallophaga and Anoplura have so many morphological features in common that it is scarcely probable that such characters have arisen independently in the two groups. Mjoberg (1910) and Harrison (1916A) have presented a detailed comparison of the two suborders, organ for organ, and contributed much towards placing their intimate phylogenetic relationships on a sound basis. The Mallophaga and Siphunculata are treated separately below.

Sub-order I. MALLOPHAGA (**Lipoptera**: Biting lice or bird lice)

INSECTS LIVING AS ECTOPARASITES MAINLY OF BIRDS, LESS FREQUENTLY OF MAMMALS. EYES REDUCED. MOUTH-PARTS OF A MODIFIED BITING TYPE: MAXILLARY PALPI 4-JOINTED OR WANTING: LIGULA UNDIVIDED OR 2-LOBED, LABIAL PALPI RUDIMENTARY. PROTHORAX EVIDENT, FREE: MESO- AND META-THORAX OFTEN IMPERFECTLY SEPARATED: TARSI 1- OR 2-JOINTED, TERMINATED BY SINGLE OR PAIRED CLAWS. THORACIC SPIRACLES VENTRAL.

The Mallophaga are very small or small (·5 to 6 mm. long), flat-bodied, active insects entirely adapted for an ectoparasitic life. The majority of the species infest birds and a smaller number occur on mammals. Unlike the Siphunculata, Mallophaga never directly suck blood but live on fragments of feathers, hair, and other epidermal products. Their food consequently consists of dry and nearly or quite dead cuticular substances, which they bite off by means of their strong sharp-edged mandibles. They do not, however, neglect casual opportunities of imbibing blood as, for instance, when a bird is shot.

When birds are badly infested with Mallophaga bare areas of the skin often appear where the feathers have been eaten through, or fallen out. The greatest amount of injury entailed by the hosts apparently does not come from the feeding habits of these insects, but from irritation of the skin, caused by the scratching action of the claws of the feet, during the migrations of the lice over the body. When a single bird is infested by some hundreds of these parasites, as is frequently the case, it becomes so irritated that it takes little food or rest, grows weakly and thin, and is less able to resist disease. The dust-baths taken by poultry and many wild birds are chiefly to rid themselves of Mallophaga.

Kellogg, who is the principal authority on the sub-order, states that when a bird is shot, the Mallophaga on it die from two hours to two or three days afterwards: in rare cases living lice are found on the drying bird-skin after one week. On such a likely place as an ocean rock, from which he had just scared away hundreds of perching sea-birds, no Mallophaga could be found. Migration therefore probably takes place while the bodies of the hosts are in contact. The whole existence of these insects is passed upon the body of the bird or mammal, the temperature of which is relatively constant. Their life-histories are very simple. The small elongate eggs are glued separately to the feather or hair, as the case may be, and from them the nymphs very soon hatch. The young closely resemble their parents except in size, and to some degree in markings, and they partake of the same kind of food. They moult several times and in a few weeks attain maturity. Both Kellogg and Harrison have commented on the very remarkable correspondence which exists between certain of the species-groups of these insects coming from definite host-groups. Thus, the Mallophagan parasites of hawks, ducks, pigeons or shore-birds constitute well-defined groups, the distribution of which is confined to, in most cases, a single host-order. Kellogg comes to the conclusion that the near relationship of hosts, in cases of parasitic species under circumstances eliminating the possibility of migration from one host-species to another, is due to the persistence of the parasitic species unchanged from the time of the common ancestor of the two or more, now distinct but closely allied, species or even genera of birds. Owing to their uniformity of food and habit, and the absence of apparently any marked struggle for existence, the stimulus to a rapid differentiation among Mallophaga is wanting.

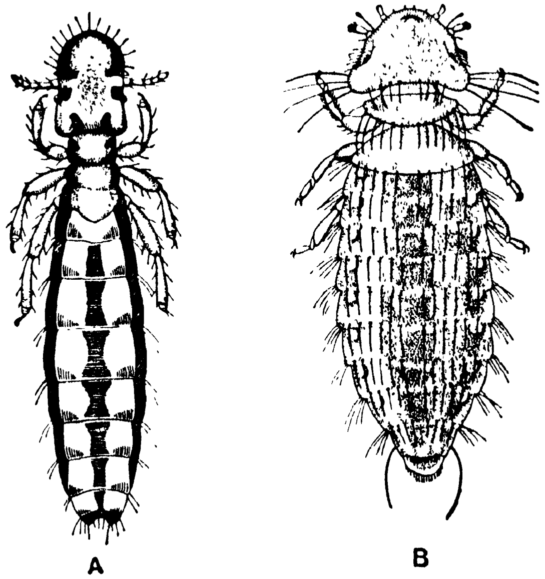

FIG. 311. MALLOPHAGA OF DOMESTIC FOWL.

A, *Lipeurus caponis* L. *After* Denny. B, *Menopon pallidum* Nitz. *After* Bishop and Wood, U.S. Farmer's Bull., 801.

It has been suggested that these insects might possibly prove of some aid in bird-phylogeny. Thus Harrison (*Parasitology*, 1915) finds that *Ptericola*, which is a normal parasite of the ratite bird *Apteryx*, is at most only a sub genus of *Rallicola* which is a universal parasite of rails. The Mallophaga of the remaining Ratitæ have nothing in common with those of *Apteryx*. The inference which he draws from these conclusions is that *Apteryx* is more closely related to the Ralli than to any other living birds. The possibility of this relationship has been independently foreshadowed by such authorities on avian morphology as Fürbinger and Gadow.

The most notorious member of the order is the common chicken-louse *Menopon pallidum*. Ducks are infested by several species, among which a common form is *Philopterus dentatus*. Pigeons are almost always infested by an elongate and very slender louse, *Lipeurus baculus*. The species living on domestic mammals belong to the genus *Trichodectes*: thus the dog is often infested by *T. canis* and cats by *T. subrostratus*. Horses and donkeys harbour several species while *T. bovis* troubles cattle all over the world. Comparatively few species of *Trichodectes* have been recorded from wild mammals but they have been found on such dissimilar animals as bears, porcupines, beavers and deer.

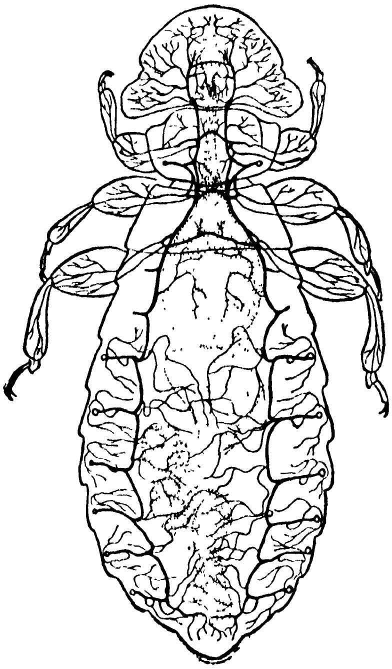

Fig. 312. Tracheal System of *Myrsidea cucularis*.

After Harrison, *Parasitology*, 8.

External Anatomy.—The body is usually very much flattened dorso-ventrally with the integument well chitinized. Over the abdomen the tergal, pleural, and sternal regions are separated by very distinct areas of membrane. The *head* is large and horizontal, and situated closely upon the prothorax. The *antennæ* differ very markedly in the two sub-orders: in the Amblycera they are generally capitate, and concealed in deep fossæ, while among the Ischnocera they are filiform and exserted. The *mouth-parts* (Snodgrass, 1896; 1905) are of the biting type with large dentate *mandibles*, which differ in their insertion in the two sub-orders (Fig. 313). Among the Amblycera they lie parallel with the ventral surface of the head, so that each condyle is ventral and the ginglymus dorsal. In the Ischnocera each mandible is inserted more or less at right angles with the head, the condyle being posterior and the ginglymus anterior. The *maxillæ* are single-lobed and lack differentiation into the usual sclerites: they are, furthermore, attached to the lateral margins of the labium and, for this reason, their palpi were formerly regarded as belonging to that region. In certain genera a pair of minute forked rods have been described, but are very fragile and easily overlooked. They are evidently homologous with similar, but more prominent, organs which are characteristic of the Psocida. The maxillary palpi are 4-jointed in the Amblycera and wanting in the Ischnocera. The *labium* is composed, basally, of a submentum and mentum; the palpi are reduced to small lobes, and the ligula is either entire or represented by a pair of fleshy processes, probably homologous with paraglossæ. One of the most characteristic buccal organs is the *œsophageal sclerite* (vide

Cummings, 1913) which is a greatly developed thickening of the chitinous lining of the anterior part of the œsophagus. The body of it is shield-shaped or oval with a pair of antero-lateral arms. A complex type of *hypopharynx* is present and associated with it, in most genera, is a pair of ovoid plates with rod-like stalks. The ovoid plates have often been termed lingual glands, but direct evidence of their possessing any glandular structure is not forthcoming. They closely resemble the corresponding parts in the Psocoptera, and are regarded by Enderlein (1903) as being superlinguæ. A curious trachea-like structure arises from the œsophageal sclerite and divides into two branches, one branch uniting with each of the plates previously alluded to.

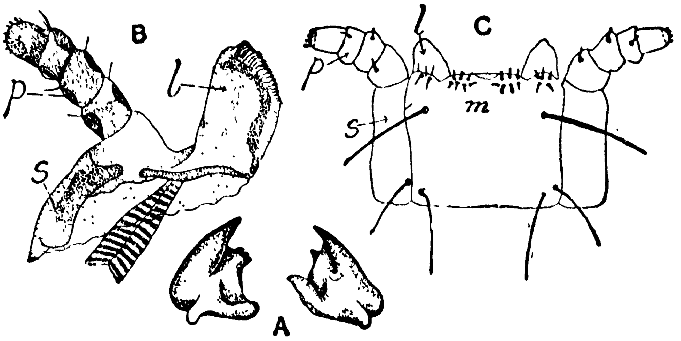

FIG. 313. MOUTH-PARTS OF *MALLOPHAGA*. A, mandibles. B, maxilla (*Læmobothrium*). C, labium and maxillæ (*Ancistrona*).

l, maxillary lobe; *m*, mentum; *p*, maxillary palp; *s*, stipes. Adapted from Snodgrass 1899, 1905.

In the *thorax*, the meso- and metanota are frequently united, but among the Amblycera a sutural line separates the two segments. The legs are very similar throughout the order and the tarsi commonly bear a pair of claws, but in *Trichodectes* and *Gyropus*, which infest mammals, the claws are single.

The number of abdominal segments in the adult is usually nine, although ten may be present during post-embryonic development. The genital opening in both sexes is situated within a chamber formed by the invaginated body-wall. Genitalia are wanting in the female but, in the male, the ædeagus is often an organ of complex structure, and the genitalia are formed as chitinizations of its walls (vide Snodgrass, 1899).

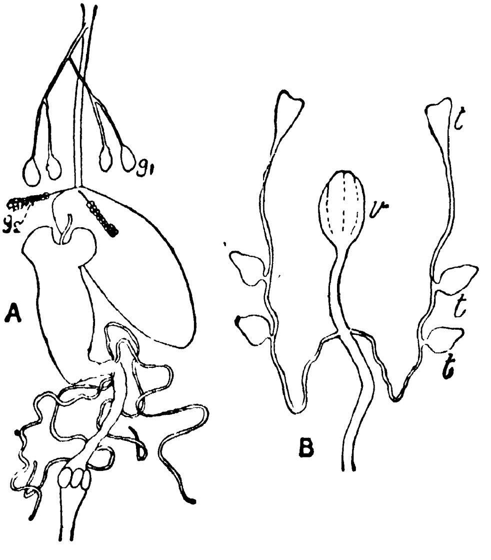

FIG. 314. A, digestive system of *Eurymetopus taurus*.

*g*1, salivary glands; *g*2, supplementary glands.

B, male reproductive organs of *Physostomum diffusum*.

t, testis; *v*, vesicula seminalis. *After* Snodgrass, *Occas. Papers Calif. Acad. Sci.*, 1899.

Internal Anatomy.—A general description of the internal organs is given by Snodgrass (1899). The *alimentary canal* (Fig. 314A) is either an almost straight tube, or slightly convoluted, but always comparatively short. It is characterized by the well-developed crop, the large mid-intestine, and short simple hind-intestine. A pair of large enteric cœca extend as outgrowths of the stomach on either side of the crop. There are four Malpighian tubes and a whorl of six prominent rectal papillæ. Among the Amblycera, the crop is a simple expansion of the œsophagus: in the Ischnocera it is greatly developed, and is either connected with the gut by means of a narrow duct-like tube, as in *Trichodectes*, or assumes a more or less fusiform shape, and extends into the body-cavity to one side of the alimentary canal. *Salivary glands* are well developed and consist of two pairs, or of one pair of glands and a pair of reservoirs. In either case, they are situated alongside the fore intestine, and the two pairs of ducts unite to form a common canal opening into the floor of the pharynx. Among the Ischnocera there is also a pair of supplementary glands whose ducts open one on either side into the œsophagus at the mouth of the duct of the crop, or directly into the latter organ. The *nervous system* is highly specialized: in *Eurymetopus taurus* the brain is laterally expanded in such a manner as to be U-shaped, the subœsophageal ganglion is exceptionally large, and is united with the thoracic chain by means of short thick connectives. The thoracic ganglia are three in number and connectives are wanting: there are no ganglia in the abdomen, the latter region being innervated from the metathoracic ganglion. The *tracheal system* (vide Harrison, 1915) is disposed in two main trunks, opening to the exterior by means of seven pairs of spiracles (Fig. 312): of the latter, the first pair is prothoracic, and the remainder are abdominal and situated typically on segments 3 to 8 or, more rarely, on segments 2 to 7. In *Trimenopon* and *Gliricola* there are five pairs of abdominal spiracles located on segments 3 to 7. The *heart* (vide Fulmek, *Zool. Anz.* 29) is situated in the 7th and 8th or 8th segment of the abdomen. It is an extremely short chamber provided with 2 or 3 pairs of ostia, and is continued forwards as the aorta: the latter is swollen into a bulbus arteriosus at its junction with the heart. The *female reproductive organs* consist of a pair of ovaries, each organ being usually composed of five panoistic ovarioles: in the Amblycera there is a tendency to reduction, and the ovarioles may be restricted to three. The common oviduct leads into a vagina and the latter opens behind the 7th sternum. In *Eurymetopus* a globular accessory gland and a spermatheca communicate with the vagina, but both organs are wanting, for example, in *Menopon*. With regard to the *male reproductive organs* (Fig. 314B), the testes are composed of three (Amblycera) or two (Ischnocera) ovoid or pyriform follicles, which are quite separate from one another. Those of a side communicate with the corresponding vas deferens, and the two latter canals frequently discharge into the vesicula seminalis. This organ is compact and bilobed, often large, and is continuous distally with a tortuous ejaculatory duct.

Classification.—About 1,700 species of Mallophaga are known, and for their taxonomy reference should be made to the important works of Piaget (1880) and Kellogg (1908). Harrison (1916) has contributed a revised list of the genera and species of the world, and the British species have been monographed in the now antiquated volume of Denny (1842). Descriptions of the more important species affecting domestic animals will be found in textbooks of parasitology, notably those of Raillet, Neumann, Neveu-Lemaire and others.

The Mallophaga fall into two well-defined superfamilies and four principal families. For a recently erected third group, see p. 316.

Superfamily I. **Amblycera.**—ANTENNÆ CAPITATE, 4-JOINTED, CONCEALED. MANDIBLES HORIZONTAL. MAXILLARY PALPI 4-JOINTED. MESO- AND META-THORAX WITH A SUTURAL LINE USUALLY VISIBLE.

(1)—Tarsi single-clawed; infesting mammals. *Gyropus*. **GYROPIDÆ**

(2)—Tarsi with paired claws; infesting birds (with a few exceptions). *Menopon* (Fig. 311B), *Trinoton*. **LIOTHEIDÆ**

Superfamily II. **Ischnocera.**—ANTENNÆ FILIFORM, 3 to 5-JOINTED, EXPOSED. MANDIBLES VERTICAL. MAXILLARY PALPI WANTING. MESO- AND META-THORAX USUALLY FUSED.

(3)—Antennæ 5-jointed; tarsi with paired claws; infesting birds. *Docophorus, Lipeurus* (Fig. 311A), *Goniodes*. **PHILOPTERIDÆ**

(4)—Antennæ 3-jointed; tarsi single-clawed; infesting mammals. *Trichodectes*. **TRICHODECTIDÆ**

Sub-order II. **SIPHUNCULATA** (**Anoplura** of most writers: Sucking Lice.)

INSECTS LIVING AS ECTOPARASITES OF MAMMALS. EYES REDUCED OR ABSENT. MOUTH-PARTS HIGHLY MODIFIED FOR PIERCING AND SUCKING, RETRACTED WITHIN THE HEAD WHEN NOT IN USE. THORACIC SEGMENTS FUSED: TARSI 1-JOINTED, CLAWS SINGLE. THORACIC SPIRACLES DORSAL.

The insects included in this sub-order are exclusively blood-sucking ectoparasites of mammals and somewhere about 200 species have been described. Of these, two species infest man and about a dozen occur on domestic animals: the remainder have been taken from a wide range of mammals including monkeys, rabbits, mice, seals, elephants, etc. There is no doubt that the greater number of species are, as yet, undescribed and only a beginning has so far been made in the study of these insects.

Kellogg (*Science*, 1913, p. 601) has discussed the close physiological relationships between certain of these parasites and the specific blood characters of their hosts. Work by means of precipitin tests, and the study of the crystallizable proteins (hæmoglobin), has emphasized the similarity of the blood in closely related mammals, and its dissimilarity in the more distantly related species. The conclusions derived from these lines of investigation are supported by the very definite host-relations of these parasites.

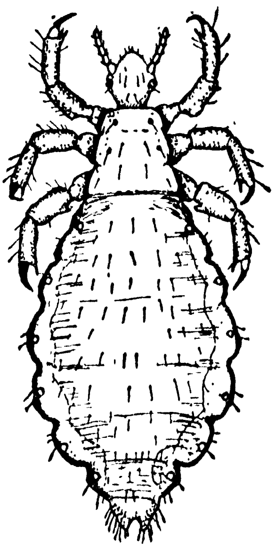
FIG. 315. BODY LOUSE (*PEDICULUS HUMANUS*), FEMALE, MAGNIFIED.

The best known species of Siphunculata is *Pediculus humanus* L., the common louse of man (Fig. 315). It infests people living under unhygienic conditions and who, through neglect or force of circumstances, go for a number of days without any change of clothing. This insect exists in at least two races which were formerly regarded as separate species; they are *P. humanus capitis* de G., the head louse, and *P. humanus corporis* de G. (*vestimenti Nitz.*), the body louse. Of the two races, typical examples of *capitis* are the smaller and darker, the antennæ are thicker and the divisions between the abdominal segments more strongly marked. This race occurs on the head, laying its eggs on the hair. The race *corporis* is typically composed of larger individuals, which are paler than *capitis*, with the antennæ more slender, and the divisions between the abdominal segments less pronounced. It occurs more especially among the folds and seams of underclothing, passing to the skin when it desires to feed: the eggs are either laid in the clothing or attached to the body hair. The two races interbreed freely under experimental conditions and are known to be fertile through several generations. Furthermore, when the race *capitis* is reared under conditions suited to *corporis* it loses its distinctive morphological characters and, after four or more generations, acquires those of the latter race. There is reason to believe that *capitis* is the more primitive race and that *corporis* is derived from it in adaptation to the acquisition of clothing by its host.

The louse lays up to about 300 eggs, which are usually deposited at the rate of 8 to 12 daily. Each egg is fastened to a hair or fibre, by means of a cementing substance, and the young insect emerges by pushing open an operculum at the anterior pole. It appears that, with the natural body-heat of the host, when there is no change of clothing next the skin, the incubation period is about a week. Three ecdyses occur during the life of the insect, and development is one of simple growth, unaccompanied by any changes sufficiently pronounced to constitute metamorphosis. The length of the life-cycle is dependent upon temperature, facilities for feeding, etc.: probably on an average about seven weeks intervene between the time of hatching and the death of the adult insect.

Pediculus humanus is concerned with the transmission of more human diseases than any other insect. Typhus fever is the most virulent of these maladies and its causative organism is carried by both races of the louse. If the insect imbibes blood from a typhus patient, in 7 to 11 days afterwards, it is capable of transmitting the disease to another human being by means of punctures of the skin made by the mouth-parts. Subsequent research has demonstrated that the excreta of infected lice may also cause infection, through abrasions of the skin, and the crushed bodies of lice may transmit the disease in a similar manner. During the European War, 1914–19, the complaint known as trench fever occurred in practically all the chief areas of fighting, and it has been proved to be transmitted indirectly by this insect. The malady is chiefly spread by the excreta of the louse which contain large numbers of the causative agent. The disease appears to be usually contracted by the excreta of the insect infecting abrasions of the skin, but a healthy human being may even contract the complaint should the dried excreta come in contact with the eye membranes, while clothes, etc., are being shaken. Relapsing fever can also be conveyed to man by the louse and, should an example of the latter containing the spirochæte of this disease in a particular phase of development, be crushed upon the skin, which is commonly excoriated by the self-inflicted scratches of the individual harbouring lice, that individual can in this manner become infected. This disease, similarly to trench fever, is not known to be directly transmitted by the punctures of infected lice. During the last ten years the literature on *Pediculus humanus* has assumed extensive proportions. For a general account of its biology and relation to disease, vide Lloyd (1918) and the papers of Nuttall (1917, 1917A, 1917B, 1919), also recent works on medical entomology. So far as known the genus comprises this species only, which is confined to man and certain monkeys and apes. *P. schaffi* Fahren., from the chimpanzee, and other reputed species, are probably to be regarded as races of *P. humanus*.

The only other genus of Siphunculata infesting man is *Phthirus*, whose single species *P. pubis* Leach is commonly known as the crab louse. This insect is usually confined to the pubic and peri-anal region and is not known to serve as the vector of any infective disease. The eggs resemble those of *Pediculus* in their general features and method of attachment to the body-hairs. According to Nuttall (1918) the eggs hatch *in situ* in six to eight days, the insects pass through three ecdyses, and the total life-cycle from the time the eggs are laid until the adults are mature and ready for oviposition is 22 to 27 days.

Among other genera of the sub-order one of the most prevalent is *Hæmatopinus* which is mostly parasitic upon ungulates: *H. suis* (Fig. 319) is the well-known hog louse which occurs on domestic and wild pigs in many parts of the world (vide Florence, 1921): *H. tuberculatus* is found on the buffalo in E. Europe and the orient, and *H. eurysternus* occurs on domestic cattle and may, at times, prove a pest. Species of *Polyplax* find their hosts among the Muridæ, and *P. spinulosus* transmits *Trypanosoma lewisi* from rat to rat. *Echinopthirius*, and its allies, exclusively infest marine mammals (seals, sea-lions and walruses), and the anomalous genus *Enderleinellus* occurs only on Sciuridæ.

External Anatomy.—The body of a louse is dorso-ventrally flattened and only the abdomen is distinctly segmented. The head is more or less conical and pointed and, in *Linognathus*, it is much attenuated and relatively little broadened behind the antennæ. The antennæ are short and 3- to 5-jointed: in *Pediculus* and *Phthirus* they are 3-jointed in the first instar, but afterwards become 5-jointed, and in *Pedicinus* they are 3-jointed throughout life. The eyes are reduced and often aborted but are relatively well developed in *Pediculus*.

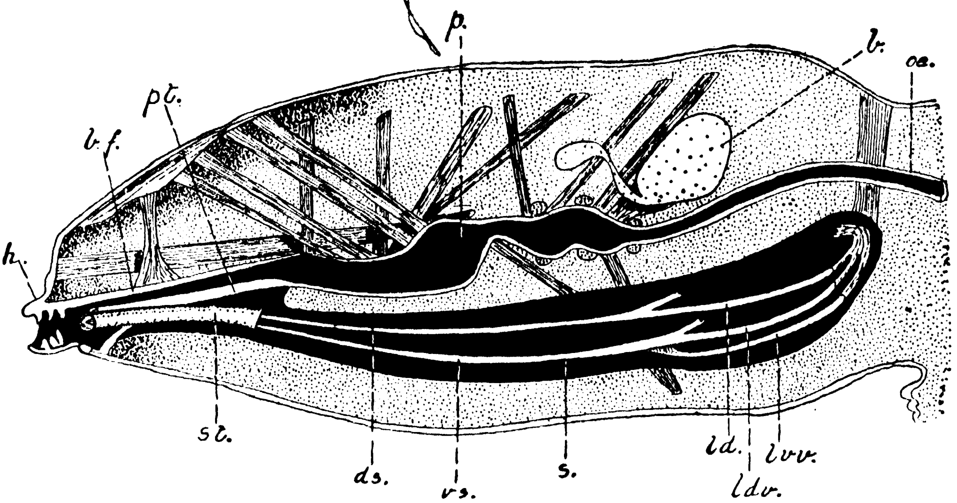

FIG. 316. DIAGRAMMATIC LONGITUDINAL SECTION OF THE HEAD OF *PEDICULUS*.

b, brain; *bf*, buccal funnel; *ds*, dorsal stylet; *h*, rostrum; *ld*, left ramus of dorsal stylet; *ldv*, *lvv*, left dorsal and ventral rami of ventral stylet; *oe*, œsophagus; *p*, pharynx; *pt*, pharyngeal tube; *s*, stylet sac; *st*, sac tube; *vs*, ventral stylet. Adapted from Peacock, *Parasitology*, 11.

The *mouth-parts* (Fig. 316) are extremely difficult to investigate owing to their minute size and delicacy of structure: they are highly modified for piercing and sucking, and little is definitely known with respect to the homologies of the various parts. They have been described by Enderlein (1904), Pawlowsky (1906), Peacock (1918), and others, but the various accounts contain many discrepancies. The description of the mouth-parts of *Pediculus* given by the last-mentioned author is largely followed in the present work. In the resting condition the mouth-parts are entirely retracted within the head and it is necessary, therefore, to refer to certain features of the internal anatomy. If a transverse section be taken across the head, in front of the insertions of the antennæ, two separate canals are seen in the middle line, one above the other. The upper canal is the fore-intestine and the lower one is the stylet-sac. The fore-intestine, in this region, is termed by Peacock the *buccal funnel*: it opens to the exterior at the apex of a very short rostrum which carries a series of denticles. When at rest the latter lie within the cavity of the rostrum, but they can be rotated outwards, so as to become external, when used to transfix the host during feeding. The buccal funnel leads into the *pharynx* which is composed of two successive chambers, the second one communicating with the œsophagus. The *stylet-sac* is a ventral diverticulum, arising anteriorly from the floor of the buccal funnel, and extending to the hinder region of the head. The mouth of the sac is prolonged forwards into the buccal funnel by means of the *sac tube,* which is a trough composed of a pair of half tubes, which are opposed to one another along their ventral edges. A pair of slender structures each likewise in the form of a half tube, arises from the floor of the first chamber of the pharynx. They fit closely together so as to form an afferent *pharyngeal tube* : anteriorly the latter is embraced by the sac-tube already referred to. The *stylets,* or stabbers, are two in number, one being situated above the other within the stylet-sac : anteriorly they rest in the sac tube, below the pharyngeal tube. The *dorsal stylet* is paired ; the halves are in close contact along the greater part of their length, but diverge where they are basally attached to the blind end of the stylet-sac. The *ventral stylet* is stated by Peacock to be composed of two superposed elements, each of which is basally attached to the stylet-sac by a pair of diverging arms. The *salivary duct* runs just beneath the dorsal stylet (Fig. 317). When the insect desires to feed its method of action is probably, in brief, as follows. The rostrum is everted and the denticles maintain hold on the skin of the host. Special muscles come into play, which draw the buccal funnel and pharynx forward, with the result that the pharyngeal tube and sac tube come into contact with the skin. The action of protractor muscles, associated with the stylets, brings the latter structures into action, and they perforate the skin : at the same time saliva enters the puncture. The pharyngeal tube is inserted into the wound and, by means of the pumping action of the pharyngeal muscles, blood from the host is sucked up.

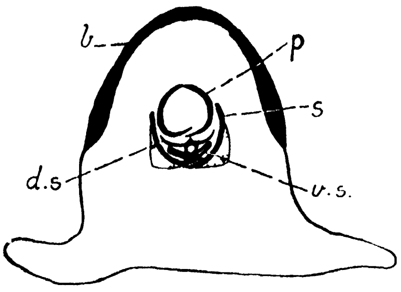

FIG. 317. TRANSVERSE SECTION OF THE BUCCAL FUNNEL OF *PEDICULUS*.

b, arch of buccal funnel; *ds*, dorsal stylet (with salivary duct just beneath); *p*, pharyngeal tube; *s*, sac tube; *vs*, ventral stylet. Adapted from Peacock, *loc. cit.*

According to Fernando (*Quart. Journ. Mic. Sci.*, 1933), embryology shows that the mandibles disappear and that the maxillæ fuse to form the dorsal stylet, the labium forms the ventral stylet and the labrum remains as the roof of the buccal funnel.

The *thorax* is relatively small and only imperfectly segmented. The legs are strongly developed in accordance with a mode of life which requires appendages adapted for maintaining a firm hold on the host. The tarsi are single jointed, and each is terminated by a powerful claw.

The *abdomen* is 9-segmented : the terga and sterna are, as a rule, thinly chitinized, while the pleura are strongly developed and deeply pigmented. A copulatory organ is well developed in the male, and in the female there is a pair of short gonopods which are used during oviposition for grasping the hair and directing the alignment of the eggs. Cerci are wanting in both sexes.

Internal Anatomy (Fig. 318).—Most of what is known concerning the internal anatomy is relative to *Pediculus* and *Hæmatopinus*. The anterior portion of the fore-intestine has already been referred to, and the œsophagus passes directly to the stomach, both crop and gizzard being undeveloped. The stomach is a large chamber which narrows posteriorly, and occupies the greater portion of the abdominal cavity: in *Pediculus* a pair of large enteric cœca is present anteriorly. The hind intestine presents no convolutions and receives four Malpighian tubes, and the rectum is provided with a whorl of six chitinized rectal papillæ. There are two pairs of salivary glands which are situated in the thorax: one pair is elongate and tubular, the other being compact and reniform: their ducts apparently combine to form the salivary canal already mentioned in relation to the mouth-parts. A pair of glands, known as Pawlowsky's glands, open into the stylet sac and their secretion possibly serves to lubricate the stylets. The *tracheal system* exhibits a general agreement with the simpler Mallophagan type (Harrison, 1915): there are usually seven pairs of spiracles, the thoracic pair being dorsal, and the abdominal spiracles open on segments 3 to 8. The *female reproductive organs* consist of five polytrophic ovarioles to each ovary and there is also a pair of accessory glands but no receptaculum seminis. The *male reproductive organs* are composed of a pair of compact bilobed testes and the slender vasa deferentia either open into a pair of tubular vesiculæ seminales (*Pediculus*) or discharge separately from the latter into the ejaculatory duct (*Phthirus*). In *Pediculus* copulation takes place at frequent intervals and this fact is probably related to the absence of a receptaculum in the female and presence of well developed vesiculæ seminales in the male: according to Bacot one male may fertilize 10 to 18 females. The *nervous system* is highly concentrated, the thoracic and abdominal ganglia being fused into a common mass.

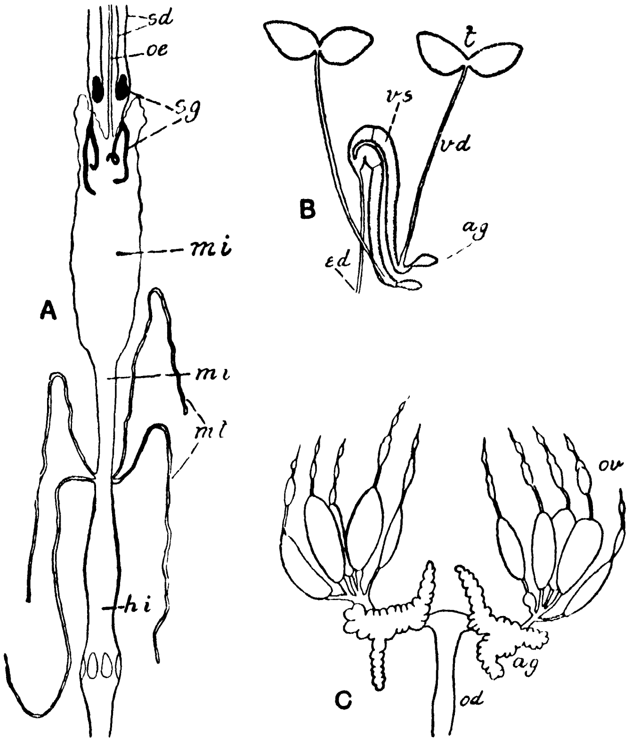

FIG. 318. *PEDICULUS*. A, digestive system. B, male and C, female reproductive organs.

ag, accessory gland; *ed*, ejaculatory duct; *hi*, hind-intestine; *mi*, mid-intestine; *od*, oviduct; *oe*, œsophagus; *ov*, ovary; *sg*, salivary glands and ducts *sd*; *t*, testis; *vd*, vas deferens; *vs*, vesicula seminalis. Adapted from Patton and Cragg.

Classification.—The Siphunculata are divided into three families as given below. A catalogue of the species and host list up to 1916 is given by Ferris, and the British species are enumerated by Denny

(1842) and more recently by Grimshaw (*Scot. Nat.* 1917). The number of species affecting our indigenous mammals is rather more than a score. Contributions towards a monograph of the sub-order by Ferris (5 parts published) will be found in *Leland Stanford Publications, Univ. Series,* 1919 to 1932.

1 (4).—Body flattened; spiracles on mesothorax and abdominal segments 3–8.
2 (3).—Pigmented eyes present; head not retracted into thorax. *Pediculus, Phthirus, Pedicinus.* **PEDICULIDÆ**
3 (2).—Eyes vestigial or absent; head retracted into thorax. *Hæmatopinus, Linognathus, Polyplax.* **HÆMATOPINIDÆ**
4 (1).—Body thick and stout; spiracles on meso- and meta-thorax and abdominal segments 2–8. *Echinopthirius.* **ECHINOPTHIRIIDÆ**

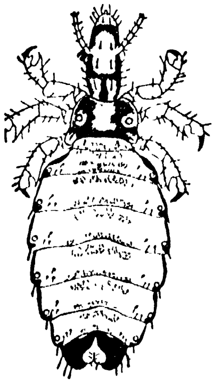

FIG. 319.—FEMALE HOG LOUSE (*HÆMATOPINUS SUIS*).

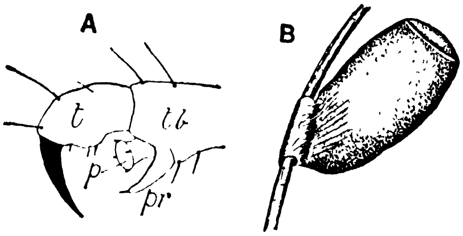

FIG. 320.—*HÆMATOPINUS SUIS.* A, extremity of leg. B, egg attached to a bristle.
t, tarsus; *tb*, tibia; *pr*, process of tibia; *p*, tibial pad.

APPENDIX TO ANOPLURA.—Ferris (*Parasitology*, 23, 1931) has recently investigated the structure of *Hæmatomyzus*, the single species of which is a parasite of the elephant and has long been regarded as a member of the Siphunculata. He points out that the mouth-parts are definitely of the mandibulate type. As regards other features, the antennæ, spiracles and genitalia are of such a character as might belong to a member of either the Mallophaga or Siphunculata while the head, thorax and legs show features different from those prevailing in either sub-order. On account of the biting mouth-parts it is evident that this genus is to be regarded as a member of the Mallophaga. Ferris proposes the name Rhyncophthirina for a new group to contain it. This name is adopted here as that of a third superfamily of the Mallophaga.

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1918.–The Biology of *Phthirus pubis*. *Ibid*. —— **1919**.–The Systematic Position, Synonymy, and Iconography of *Pediculus humanus* and *Phthirus pubis*. *Ibid*. 11. **PAWLOWSKY, 1906**.–Über den Stech und Saugapparat der Pediculiden. *Zeit. wiss. Insektenbiol*. 2. **PEACOCK, 1918**.–The Structure of the Mouth-parts and Mechanism of Feeding in *Pediculus humanus*. *Parasitology*, 11. **PIAGET, 1880**.–Les Pédiculines. Leyden. **SIDKORA, 1916**.–Beit. zur Anat., Biol. und Physiol. der Kleiderlaus. *Arch. Schiff. u. Trop.-Hyg*. 20. **SNODGRASS, 1896**.–In Kellogg's " New Mallophaga II." *Proc. Calif. Acad. Sci*. 6. —— **1899**.–The Anatomy of the Mallophaga. *Occas. Papers. Calif. Acad. Sci*. 6. —— **1905**.–A Revision of the mouth-parts of the Corrodentia and Mallophaga. *Trans. Am. Ent. Soc*. 31. **STRINDBERG, 1916**.–Zur Entwickl. und Anat. der Mallophagen. *Zeits. wiss. Zool*. 115.

Order 11. EPHEMEROPTERA (Plectoptera: May-flies)

SOFT-BODIED INSECTS WITH SHORT SETACEOUS ANTENNÆ AND VESTIGIAL MOUTH-PARTS DERIVED FROM THE BITING TYPE. WINGS MEMBRANOUS, HELD VERTICALLY UPWARDS WHEN AT REST; THE HIND PAIR CONSIDERABLY REDUCED; "INTERCALARY" VEINS AND NUMEROUS CROSS-VEINS PRESENT. ABDOMEN TERMINATED BY VERY LONG CERCI EITHER WITH OR WITHOUT A SIMILAR MEDIAN CAUDAL PROLONGATION. THE IMAGINES UNDERGO ECDYSIS BEFORE SEXUAL MATURITY. METAMORPHOSIS HEMIMETABOLOUS: NYMPHS AQUATIC, CAMPODEIFORM, USUALLY WITH LONG CERCI AND A MEDIAN CAUDAL FILAMENT: LAMELLATE OR PLUMOSE, METAMERIC, TRACHEAL GILLS PRESENT.

Existing may-flies are the remnants of a former extensive order. They are familiar insects on the margins of lakes, streams and rivers, and the association of their name with the Ephemerides of Grecian mythology expresses their brief life above water which, in certain species, lasts but a few hours. In their nymphal stages, on the other hand, they are at least as long-lived as most insects and, in some cases, this period is believed to occupy three years.

When a may-fly is about to emerge the nymph floats to the surface of the water: a fissure then appears in the dorsal cuticle, and the winged insect issues, and flies away in the course of a few seconds. At this stage the winged form is known as the *sub-imago*, and it differs from the mature imago in several features. In their general form the two stages are alike, the wings are fully expanded and spiracular respiration is established. The sub-imago may be recognized by its duller appearance, and by its somewhat translucent wings which are usually margined by prominent fringes of hairs. The passage from the sub-imago to the imago is marked by an ecdysis which is unique among insects: the sub-imago casts a delicate pellicle from its whole body, including the wings, and then issues as a fully formed imago. In the latter condition the insect presents a shiny appearance and has assumed its full coloration, the wings become transparent, while the eyes and legs attain their complete development. Among certain of the short-lived species the sub-imaginal pellicle is partially, or completely persistent in one or other sex. The males of *Oligoneuria*, for example, retain this covering on the wings, while the females of *Palingenia* and *Campsurus* do not appear to shed any part of it at all (Eaton). The sub-imaginal stage is of variable duration and there is, furthermore, some correspondence between the time spent in this stage and the duration of life of the imago. Thus, the change into the imago may occur only a few minutes after the sub-imago has emerged from the nymphal cuticle. In such cases, the life of the imago is a fugitive one, death taking place the same evening or early the following morning. In other cases the sub-imago may exist for 24 hours, or more, leading an inactive existence resting in the shade. The resulting imago in instances of this kind may live from one to several days. The short-lived species are mostly night fliers: species of *Palingenia, Oligoneuria, Ephemera,* *Hexagenia* and *Cænis* have been observed to issue about sundown in vast swarms. Such a phenomenon is frequent on the borders of the Swiss lakes, where the may-flies sometimes appear in hundreds of thousands, and are attracted in large numbers to the arc lamps near the waterside. Certain of the more conspicuous species, especially the males, exercise familiar "dances" in the air: when carrying out these evolutions a vertical up and down motion results, a fluttering swift ascent being followed by a passive leisurely fall many times repeated.

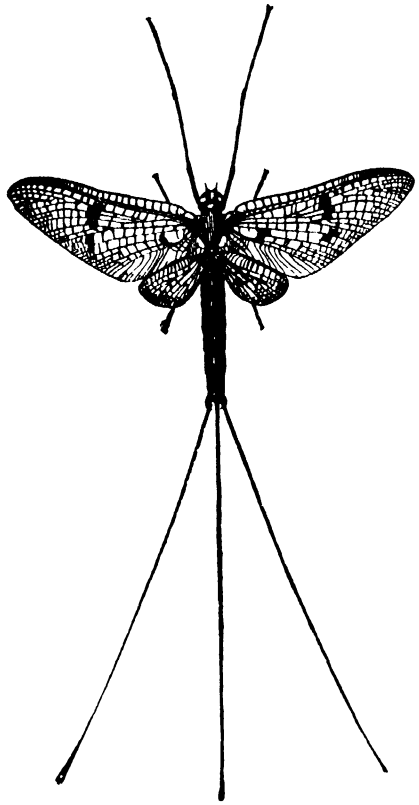

FIG. 321. *EPHEMERA VULGATA.*

(Reproduced by permission of the Trustees of the British Museum)

May-flies are eagerly devoured by fishes and most of the "duns," "spinners" and several of the "drakes," of the fly-fisher, are made up to represent various species of *Ephemera* (Fig. 321), and are used at times when the species of the latter are on the wing.

Probably between 800 and 900 species of Ephemeroptera are described but only the European and N. American representatives are at all adequately known. About 40 species occur in Britain and a synopsis of these forms is provided by Eaton (1888). The latter authority (Eaton, 1883–87) has written a monograph on the world's species and recognizes a single family—the Ephemeridæ. This work is still the standard treatise on the order and contains much general information.

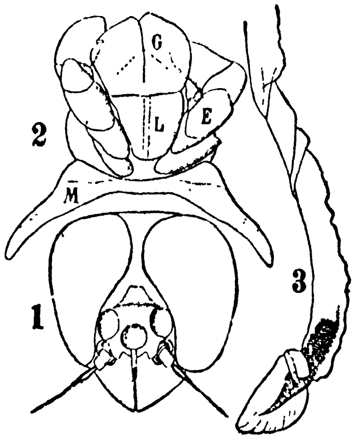

FIG. 322. *EPHEMERA.* 1, head viewed from above. 2, maxillæ and labium. 3, apex of tibia with tarsus.

E, maxilla; *G*, ligula; *L*, prementum; *M* postmentum. Adapted from Silvestri.

External Anatomy.—The head (Fig. 322) is free with the antennæ short, and composed of two basal joints, surmounted by a multi-articulate setaceous filament. The compound eyes are largest in the males and, in some genera, the upper portion of each has larger facets than the lower. In *Chlœon* the upper divisions are mounted upon pillar-like outgrowths of the head. Between the compound eyes there are three ocelli. The mouth-parts are degenerate: degeneration begins in the late nymph, it is externally complete in the sub-imago and complete in the imago. Individual parts do not undergo equal degrees of atrophy and the various genera differ very much in this respect. Mandibles are vestigial or wanting and the maxillæ though greatly reduced, usually retain their palpi: in *Ephemera* the labium is represented by the postmentum and a pair of distal lobes with small palpi. In some genera the mouth-parts have atrophied to the extent that they are scarcely recognizable. The often repeated statement that may-flies have no mouth-parts is not literally correct for all species, but they appear always to exist in such a weak or atrophied condition as to preclude the taking of any food.

The thorax is principally characterized by the great size and predominance of its middle segment, the pro- and meta-thorax both being small and comparatively insignificant. The wings are markedly triangular (Fig. 324) and fragile, durable organs not being required. As a rule they are largest in the female: the hind-wings are always small or minute and, in some genera (i.e. *Cænis*, *Chlœon*), they are completely atrophied. The fore-wings are longitudinally corrugated but are not folded, except in cases when the female is ovipositing below the water surface. The corrugation is correlated with the presence of so-called " intercalary " (accessory) veins and each vein, whether normal or intercalary, either follows the crest of a ridge, when it is termed a convex vein, or the bottom of a furrow when it is known as a concave vein. The intercalary veins are a very characteristic feature: they appear to be branches which have lost their basal connections with the remaining veins but are united with the latter by a greatly developed system of cross veins. The venation is of a very primitive type since the media retains its anterior (MA) and posterior (M) divisions in both pairs of wings, MA being basally fused with Rs (Tillyard, *Amer. Journ. Sci.* 23, 1923). The legs are exceedingly inconstant and are not used for walking. The tarsal joints vary from one to five: in the males the fore-legs are generally very elongate and, in some cases, the middle and hind pairs are vestigial.

The abdomen is evidently 10-segmented, with a reduced tergum belonging to the 11th segment. In the male there is a pair of usually 3-jointed clasping organs and, between the latter, two separate and distinct ædeagi. In the female there is no ovipositor, and the two oviducts open by separate apertures. A pair of exceedingly elongate multi-articulate cerci are present in both sexes and very commonly the 11th tergum is prolonged into a median process of similar form.

Internal Anatomy.—The most characteristic feature with respect to the internal organs is the modification of the alimentary canal for aerostatic purposes (Fritze, 1888. Sternfeld, 1907). This region no longer functions as the digestive tract, but has assumed an entirely new rôle, and has undergone certain structural changes in consequence. In the nymph the œsophagus is wide, but in the imago it becomes an extremely narrow tube and there is a complicated apparatus of dilator muscles which appears to regulate the air-content of the gut. Air is taken in or expelled through the mouth, and the stomach is modified into a kind of storage balloon: its epithelium is no longer secretory, but is converted into one of the pavement type, and the muscular coat has disappeared. The Malpighian tubes number about 40, and the first portion of the hind-intestine is modified to form a complex valve which precludes the escape of air from the stomach. In these short-lived insects it appears therefore to be more important that their specific gravity should be lessened, in order to facilitate the mating flight, rather than that they should take food, and live for a longer period. The sexual organs of may-flies are remarkable for their primitive nature. There are no accessory glands, and the gonoducts retain their paired nature in both sexes, each duct opening to the exterior separately. In the male the testes are ovoid sacs, and the two vasa deferentia each communicate with a separate penis of its side. Each ovary is composed of a large number of small ovarioles, disposed along a common tube which is continued posteriorly as the oviduct. Copulation is stated to be a momentary process and takes place in the air. The respiratory system is well developed and opens to the exterior by ten pairs of spiracles, two pairs being thoracic and eight pairs abdominal in position.

Oviposition and Post-embryonic Development.—None of the smaller orders of insects present so many variations of form and structure with regard to their eggs as are exhibited among the Ephemeroptera. These variations do not appear to be generically characteristic, since the eggs of very closely allied species may be completely dissimilar in all their features. The differences involve variations in colour, and chorionic sculpturing in the presence or absence of the micropylar apparatus; and in the form and occurrence of special anchoring filaments. A few examples in illustration of these facts may be cited from a paper by A. H. Morgan (1913). The egg of *Heptagenia interpunctata* is provided at each pole with a skein of fine yellow threads, which unravel in the water and serve to anchor it by becoming entangled with foreign objects. The egg of *Ephemerella excrucians* is white and slightly dumb-bell-shaped, with a strongly sculptured chorion, but with no anchoring filaments or micropylar apparatus. That of *E. rotunda* is yellowish and oval, with a smooth chorion, and a prominent mushroom-shaped micropylar apparatus: there are four anchoring filaments each being terminated by a knob-like structure. The ovoid eggs of *Ecdyurus* are provided with numerous short coiled filaments: after they have been in the water a little while each coil unwinds with a sudden spring, when it is seen to be terminated by a minute viscid button-like cap. The number of eggs laid by different species varies from several hundred up to about 4,000. Eaton mentions that some of the short-lived species discharge their eggs *en masse* as a pair of clusters which are laid on the water: these soon disintegrate and the eggs become scattered over the river-bed. The longer lived species lay them in smaller numbers at a time, either alighting on the surface for the purpose or descending beneath the water and depositing their eggs under stones, etc.; the insects float up again and fly away to repeat the process, or die without reappearing. According to Heymons the eggs of *Ephemera vulgata* hatch in 10–11 days at 20–25° C. In many species they require a much longer period for their development which may extend to several months: in *Chlœon dipterum* reproduction is viviparous (vide Causard, *Comp. Rend. Ac. Sci.* 123).

The nymphs have been described and figured in many species, notably by Pictet (1843), Vayssière (1882), Eaton (1883–8), Lestage (1917–1920), Needham, Morgan and others, but detailed life-history studies are almost wanting. There is reason to believe that the number of ecdyses is very high, 23 being recorded by Lubbock (1863–66) in *Chlœon dipterum*, but the observations were not commenced from the earliest stage. May-fly nymphs are essentially herbivorous, feeding upon fragments of the tissues of the higher plants, algæ, etc.; certain forms, however, are believed to be carnivorous but are exceptional. They frequent a great variety of aquatic situations: many live in concealment in the banks, some burrow in mud, while others hide beneath stones in lakes, streams, and rivers. Certain genera occur among water plants and are active swimmers, still others live in swift currents or near waterfalls, and there are some species which reside among decaying vegetation at the bottoms of ponds or ditches. This wide range of habitat is accompanied by an equal diversity of adaptive modifications and it is in the Ephemeroptera that the most complete types of the latter are met with among aquatic insects. The general shape of the body is very variable, but all are campodeiform with evident antennæ, and usually elongate multi-articulate cerci. Both compound eyes and ocelli are well developed, and most species possess seven pairs of plate-like or filamentous abdominal tracheal gills which are capable of independent movement by special muscles. The nymphs of *Ephemera* and *Hexagenia* burrow in mud or in the banks of streams; they have elongate bodies with strong fossorial legs. The first pair of gills is vestigial, and the remainder are biramous, consisting of a pair of lamellæ fringed with long filaments which are penetrated by tracheoles. When necessary the gills are carried reflexed upon the back, being protected thereby from abrasion. In *Iron*, *Epeorus*, and *Heptagenia* (Fig. 323) the body and appendages are flattened, and the nymphs of these genera are adapted for clinging to rocks in rapidly flowing water. The gills are laminate and each is provided with a basal tuft of branchial filaments. *Chlœon* and *Silphurus* have seven pairs of simple lamellæ which project from the sides of the body: the three caudal filaments are fringed with setæ and function as a kind of tail. They are active swimming nymphs living among water plants, etc. In *Cænis* and *Tricorythus* the nymphs live in an environment of mud and sand; there are six pairs of gills and the upper lamellæ of the first pair form opercula concealing the gills behind. The branchial chamber thus formed is guarded by fringes of setæ which preclude the entrance of mud or sand particles, held in suspension by the inhalent current. In *Oligoneuria* six pairs of dorsal gills are present on segments 2 to 7: each gill consists of small, thick, scale-like, non-respiratory lamina with a bunch of gill-filaments at its base. A pair of similar ventral gills occurs on the first segment and a tuft of gill filaments at the base of each maxillary

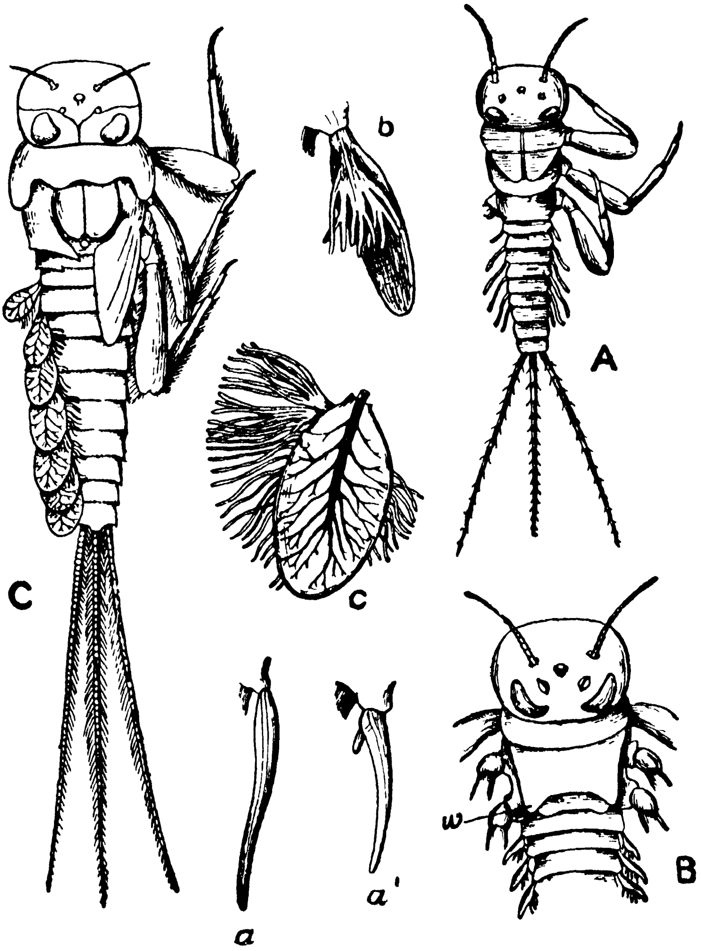

FIG. 323. NYMPHAL INSTARS OF *HEPTAGENIA*. A, third instar × 16. *a*, abdominal appendage (gill-rudiment); a^1, do. of later instar × 45. B, seventh Instar, anterior region with wing-rudiments *w*; × 12; *b*, abdominal gill. C, eighth instar with prominent wing-rudiments (on the right), × 4. *c*, abdominal gill. From Carpenter after Vayssière.

palpus. *Prosopistoma* (vide Vayssière 1890) has a most highly modified nymph which uses its body as a kind of sucker, attaching itself by this means to stones in flowing water ; it can also swim rapidly by means of its fan-like caudal filaments (Fig. 325). In this genus there are five pairs of gills located in a branchial chamber. The latter is roofed over by a carapace formed by the greatly developed pro- and meso-thoracic terga, which are fused with the sheaths of the anterior wings. The side walls of the chamber are formed by the posterior wing-sheaths, and the floor by the combined terga of the metathorax and first six abdominal segments. Water enters this very perfect type of branchial chamber by a pair of lateral apertures and the exhalent stream passes through a median opening.

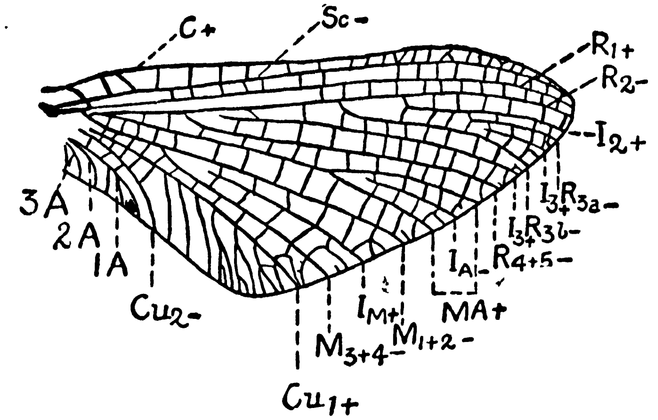

FIG. 324.—FORE-WING OF *CHIRONETES ALBIMANICATUS*

I_2, interpolated branch of R_2 I_3, I_3, interpolated branches of R_3. I_A, interpolated branch of MA. I_M, interpolated branch of media. MA, fork of anterior branch of media. (Convex veins +, concave do. -.) Venation *after* Morgan.

The morphology of may-fly nymphs has been studied in detail by Vayssière (1882) and certain of their more important anatomical features may be enumerated. Gills are commonly undeveloped in the newly-hatched nymphs: in *Ephemera* Heymons states that they arise as integumental outgrowths about the fourth day. Their usually flattened form, dorsal position and the fact that they are traversed by tracheæ have led some observers to homologize them with wings. The researches of Heymons (1896), Zimmermann (*Zeits. wiss. Zool.* 34, 1880) and of Durken (*Ibid.* 87, 1907) into their development and musculature, indicate that they are serially homologous with legs and are, therefore, to be regarded as abdominal appendages which have become adapted for respiratory needs. The groups of gill-filaments associated with the lamellate gills in many genera may also be present as outgrowths of other appendages including the legs and maxillæ.

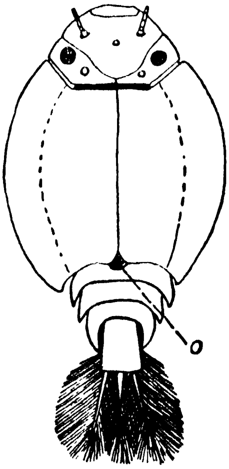

FIG. 325.—NYMPH OF *PROSOPISTOMA*.

o, exhalant aperture of branchial chamber. *After* Vayssière, *loc. cit.*

The mouth-parts are very completely formed and the peculiar mandibles are strikingly like those of the Machilidæ and of certain Crustacea ; their bases are similarly elongate, and there is a median projecting molar area, which is only wanting in the few forms which are presumably predaceous. Each maxilla has a single lobe, or mala, and a 2 to 4-jointed palp. The labial palpi are generally 3-jointed, and the ligula is conspicuously 4-lobed. The hypopharynx is very prominent and there is a pair of exceedingly well-developed superlinguæ.

The digestive system is characterized by the great size of the stomach and the large number of Malpighian tubes: the latter organs differ greatly in character among various genera. They may either open directly into the hind-intestine, or combine in groups, each group discharging into a separate pyriform sac which, in its turn, communicates with the intestine. The circulatory system is very well developed and easily observed. The dorsal vessel consists of one chamber for each abdominal segment and in the metathorax it is continued forwards as the aorta. In *Chlœon* it gives off a definite vessel into each of the caudal filaments and the terminal chamber acts as a pumping organ driving the blood into these organs: here it escapes by means of orifices in the walls of the vessels, and flows into the cavity of each filament, probably absorbing oxygen from the surrounding water.

The nervous system presents varying degrees of fusion with respect to the ganglia of the ventral chain. The brain is small but, correlated with the presence of compound eyes, the optic nerves and ganglia are well developed. In *Tricorythus* there are three thoracic and seven abdominal ganglia; in *Oniscigaster* the abdominal ganglia are reduced to six and the last two centres are closely united. In *Prosopistoma* the ganglia are fused into a common thoracic-abdominal centre; the latter genus, it may be added, is highly specialized in other directions also (Vayssière, 1890).

Classification.—The order is classified into thirteen families and the synopsis given below is based upon the revised classification of Ulmer (*Peking Nat. Hist. Bull.* 7, 1933).

Superfamily I. **Ephemeroidea.** M_{1+2} and Cu_1 of fore-wing diverging strongly at base: hind-tarsi with 4 movable joints or less, if a 5th joint present it is fused with tibia.

1 (2).—Sc of fore-wing hidden in a fold and only visible at base; wings dull and translucent; legs of female short and weak; 2 caudal filaments. **Palingeniidæ.**
2 (1).—Sc of fore-wing visible throughout its length.
3 (4).—Wings translucent in male; opaque in female; hind margin of wings without intercalary veins; legs weak, fore-legs sometimes long in male, hind-legs short and weak. **Polymitarcidæ.**
4 (3).—Wings transparent and glistening; numerous intercalary veins at hind margins, especially of posterior wings; legs strong.
5 (6).—Cu_1 of fore-wing not forked, connected with margin by veinlets; fork of R_2 and R_4 in hind-wing longer than its stem. **Ephemeridæ.**
6 (5).—Cu_1 of fore-wing forked, not connected with margin by veinlets; fork of R_2 and R_4 in hind-wing not longer than its stem. **Potamanthidæ.**

Superfamily II. **Bætoidea.** M_{1+2} and Cu_1 of fore-wing parallel at their bases; hind tarsi with 4 movable joints, if a 5th joint present it is fused with tibia.

1 (8).—Sc of fore-wing entirely visible and separated from R.
2 (7).—MA in fore-wing clearly forked.
3 (6).—Wings clear with many cross veins; hind-wings seldom absent.
4 (5).—Cu_2 in fore-wing separated from Cu_1 at base, but lying close to 1A: no free intercalary veins between M and Cu. **Leptophlebiidæ.**
5 (4).—Cu_2 in fore-wing close to Cu_1 at base, but widely separate from 1A; usually 2 free intercalary veins between M and Cu. **Ephemerellidæ.**
6 (3).—Wings milky, fringed on hind margin, often with but few cross veins: hind-wings absent (sometimes present in subimago): small species. **Cænidæ.**
7 (2).—MA in fore-wing not forked; wings clear; fore-wings with few cross veins; hind-wings small and narrow or absent. **Bætidæ.**
8 (1).—Sc of fore-wings not visible, or visible at base only, fused with R or absent: wings milky or greyish with simplified venation: cross veins limited to anterior part of fore-wings. **Oligoneuridæ.**

Superfamily III. **Heptageneoidea.** M_{1+2} and Cu_1 or fore-wing parallel at their bases; hind tarsi with 5 free joints.

1 (2).—Fore-wing with Cu_1, Cu_2 and 1A somewhat parallel and equal in length: hind-wing almost circular, with many long intercalary veins: pronotum very small. **Bætiscidæ.**

2 (1).—Fore-wings with Cu_1 and Cu_2 close at base but strongly divergent distally: Cu_2 much shorter and more strongly curved than Cu_1; hind-wing oval.

3 (4).—Cu_1 of fore-wing with more or less oblique, sinuous veinlets passing to wing margin. **Siphlonuridæ.**

4 (3).—Cu_1 of fore-wing without such veinlets; 2 or 4 parallel unattached intercalary veins in cubital area.

5 (6).—With one pair of intercalary veins between Cu_1 and Cu_2; sometimes vestiges of a 2nd pair lying near Cu_2; 2 or 3 caudal filaments. **Ametropodidæ.**

6 (5).—With 2 pairs of intercalary veins between Cu_1 and Cu_2, the larger pair near Cu_2; 2 caudal filaments. **Ecdyonuridæ.**.

(The imago of *Prosopistoma* is imperfectly known, but probably belongs near to the Cænidæ.)

Literature on Ephemeroptera

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Order 12. ODONATA (Paraneuroptera; Dragonflies)

PREDACEOUS INSECTS WITH BITING MOUTH-PARTS AND TWO EQUAL OR SUB-EQUAL PAIRS OF ELONGATE, MEMBRANOUS WINGS: EACH WING WITH A COMPLEX RETICULATION OF SMALL CROSS-VEINS AND USUALLY A CONSPICUOUS STIGMA. EYES VERY LARGE AND PROMINENT; ANTENNÆ VERY SHORT AND FILIFORM. ABDOMEN ELONGATE, OFTEN EXTREMELY SLENDER: MALE ACCESSORY GENITAL ARMATURE DEVELOPED ON 2ND AND 3RD ABDOMINAL STERNA. NYMPHS AQUATIC, HEMIMETABOLOUS: LABIUM MODIFIED INTO A PREHENSILE ORGAN: RESPIRATION BY MEANS OF RECTAL OR CAUDAL GILLS.

Rather fewer than 3,000 species of these elegant insects have been described, and they are included in about 480 genera. They attain their greatest abundance in the neotropical region and, with the exception of Japan, no part of the palæarctic zone contains an abundant or striking dragonfly fauna. Although entirely aquatic in their early stages, the imagines are by no means confined to the proximity of water, and the females of many groups seldom fly over such situations except for pairing or oviposition. They are essentially sun-loving insects but exceptions occur in some oriental species, which are only known to fly at night. Many are exceedingly swift on the wing and, according to Tillyard, *Austrophlebia* can fly at a speed of nearly 60 miles per hour: other species, particularly those of *Calopteryx* and *Agrion*, possess feeble powers of flight and may be caught with the greatest ease. Although no existing member of the order can compare in size with the Upper Carboniferous *Meganeura*, which has a wing expanse of over two feet, the females of *Megaloprepus cœrulatus* Drury measure about 190 mm. (7½ in.) from wing to wing.

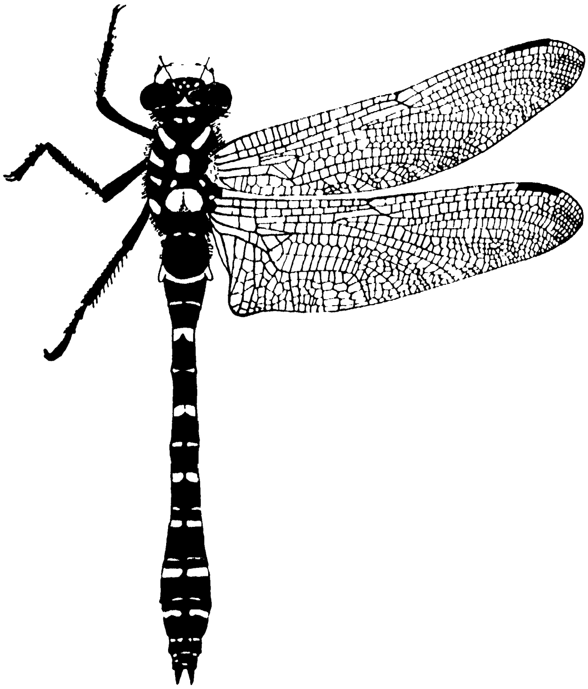

FIG. 326. AN ANISOPTERID DRAGONFLY (*CORDULEGASTER ANNULATUS*) MALE. Britain.

Probably nowhere have Odonata attracted so much attention as in Japan, where representations of these insects in art, and allusions thereto in literature, are very numerous: many of the species were recognized individually by the populace and known by vernacular names long before entomologists began to study them. Comparatively little information exists as to the food of different species of these insects. It is captured on the wing and held by the prehensile legs while being devoured. Most orders of winged insects are preyed upon, including other Odonata, Hymenoptera and Coleoptera (vide Campion, *Ann. Mag. Nat. Hist.* 1914; Poulton *Trans. Ent. Soc.*, 1906). Tillyard has recorded species preying upon Culicidæ towards dusk, and Fraser states that the latter insects are captured by certain night-flying Odonata. Although the great majority of the order seldom travel far from their restricted haunts, certain species possess strong migratory instincts, more especially the European *Libellula quadrimaculata*. Great swarms of the latter insect have frequently been recorded and they sometimes travel many miles out to sea. *Hemicordulia tau* has been noted by Tillyard occasionally to swarm in a like manner in Australia.

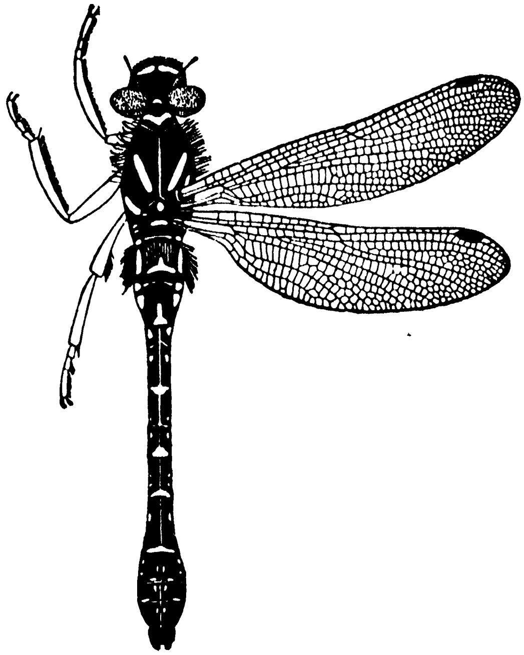

FIG. 327. *EPIOPHLEBIA SUPERSTES*, FEMALE. Japan. Adapted from De Selys with the wing-venation after Munz.

Odonata are noted for the beauty and brilliancy of their coloration and no order equals them in the wonderful development of body colours. In addition to pigmentary and structural colours, a whitish or bluish pruinescence is often present, especially in the males. It appears to be correlated with the maturation of the gonads and is exuded through fine cuticular pores, appearing as a kind of " bloom " as on certain fruits. Since it is of the nature of an exuded supra-cuticular pigmentation it is easily removed by rubbing and wear. In the female it is much less frequent and develops at a later period in life.

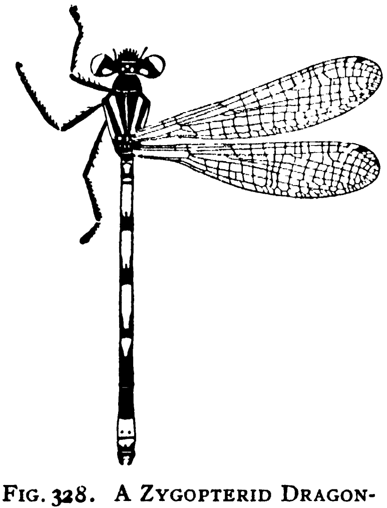

FIG. 328. A ZYGOPTERID DRAGONFLY (*AGRION PUELLA*), MALE. Britain.

Among dragonflies a bicolorous pattern is the most primitive, unicolorous forms being a later development. Many unicolorous males have bicolorous females, and newly emerged members of the former sex often exhibit traces of an original bicolorous marking for a shorter or longer period. Among the tribe Agrionini the females are often dimorphic, and one or other colour form may closely resemble the male. In the common *Ischnura elegans*, for example, the predominating or normal colour form of the female is extremely like that of the male: the rarer or "heteromorphic" females are conspicuously marked with orange, which is wanting in the normal form. Most Odonata possess hyaline wings but there are, however, certain groups which have conspicuously coloured alary organs. Thus among species of *Calopteryx* the males have metallic blue or green wings. In the Australian and E. Indian *Rhinocypha* the metallic coloration reaches its maximum and consists of a combination of glistening reds, mauves, purples, bronzes and greens utterly baffling description (Tillyard). In *Rhyothemis* the wings are also exquisitely coloured with metallic green, purple or bronze.

Odonata are represented in the British Isles by 42 species (vide Lucas, 1900) while there are several others whose inclusion in the fauna is open to doubt. The best general work on the order is that of Tillyard (1917) which has been invaluable in preparing the present chapter: the work of Ris (1909) on the German species should also be consulted.

The Imago

External Anatomy.—The form of the HEAD (Fig. 329) in dragonflies has become modified in correlation with the great development of the *eyes*. The latter, in many Anisoptera, meet mid-dorsally and compose by far the largest part of the cephalic region: in the Zygoptera the eyes are much smaller and button-like, but their range of vision is increased by the transversely elongated head. The *antennæ* are always very short and inconspicuous: they are composed of 3 to 7 joints, the latter number being usual, and have poorly developed sense organs. Experiments in amputating one or both antennæ have been made by Tillyard who finds that the insects suffer no inconvenience by their removal, and fly with the usual facility. The reduction in the development of these organs is correlated with the increased power of the compound eyes. The *mouth-parts* (Fig. 330) are entirely of the biting and masticatory type. The *mandibles* are stout with exceedingly powerful teeth, and the 1*st maxillæ* each carry a lobe-like unjointed palpus and a dentate mala. The morphology of the *labium* has given rise to considerable controversy. On referring to Fig. 330 it will be seen that the prementum is expanded by the development of side-pieces or *squamæ* and each squama carries the *lateral lobe* of its side. The inner border of each lobe terminates in an *end hook* and slightly external to the latter is a small *movable hook*. The prementum carries a single distal lobe or *ligula* which is often medianly cleft. In the Libellulidæ the movable hook is wanting, the end hook and median lobe are vestigial, while the two lateral lobes are greatly developed.

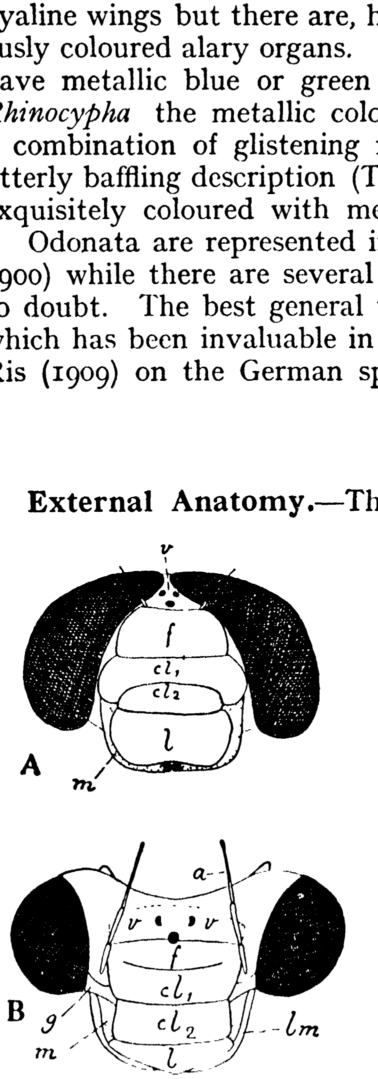

FIG. 329. HEAD OF A, ANISOPTERA: B, ZYGOPTERA.

a, antenna; *cl*$_1$, post-clypeus; *cl*$_2$, ante clypeus; *f*, frons; *g*, gena; *l*, labrum; *lm*, labium; *m*, mandible; *v*, vertex.

The head is exceptionally mobile and attached to an exceedingly small slender neck region which is supported on either side by four cervical sclerites.

The prothorax, though greatly reduced, remains a distinct segment while the meso- and meta-thorax are intimately fused together. The two latter segments are peculiarly modified in conformity with the requirements of the legs and wings (Fig. 331). The legs have shifted their attachments anteriorly and the sterna have migrated along with them. The wings, on the other hand, have moved posteriorly and the terga have shifted likewise. ✓ Although the sterna and terga of these segments are reduced their pleura are very greatly developed. The mesepisterna extend forwards and dorsalwards so as to meet in front of the mesotergum to form the dorsal carina: by this means the terga are pushed backwards and lie between the wing bases. The metepimera on the contrary have grown downwards and backwards, usually fusing ventrally behind the metasternum. In this way the sterna become pushed forwards and the legs come to lie close behind the mouth, being enabled thereby readily to hold the prey. The legs are unfitted for walking but are of some value for climbing, and the tarsi are 3-jointed.

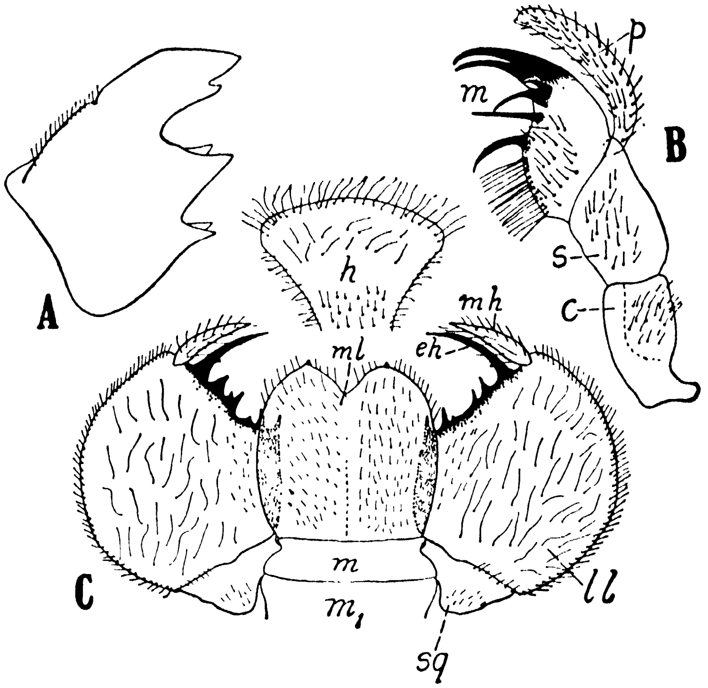

FIG. 330. MOUTH-PARTS OF *CORDULEGASTER ANNULATUS.*

A, left mandible. B, left maxilla (ventral), *c*, cardo; *s*, stipes *m*, mala, *p*, palp. C, labium and *h*, hypopharynx; *m*, prementum, *m*₁, postmentum; *ml*, median lobe (ligula), *ll*, lateral lobe (palp) with *eh*, end hook and *mh*, movable hook; *sq*, squama (palpiger).

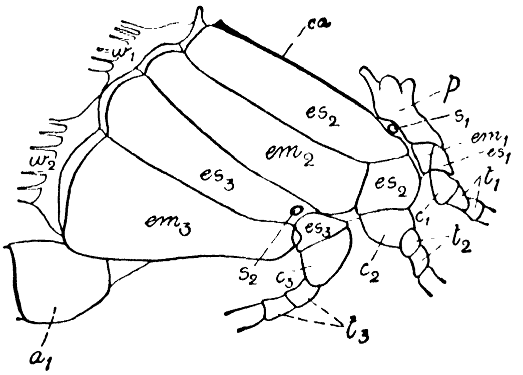

FIG. 331. LATERAL VIEW OF THORAX OF *CALOPTERYX VIRGO.*

*a*₁, 1st abdominal segment; *c*, coxa; *ca*, dorsal carina; *em*, epimeron; *es*, episternum (*es*₂ and *es*₃ are divided into supra- and infra- episternum); *p*, pronotum; *s*, spiracle; *t*, trochanter (double); *w*, wing.

The WINGS (Figs. 332 and 333) exhibit but slight diversity of form and size in the two pairs, while in the Agrionidæ they are almost identical. The veinlets are developed to a remarkable degree and form a complex reticulum, giving rise to a large number of often minute cells. In a single wing of *Neurothemis* according to Tillyard there are over 3,000 cells. A very characteristic feature is the stigma which is formed by a thickening of the wing membrane between C and R. This structure is greatly elongated in *Petulura,* almost square in *Ischnura* while in *Calop* *teryx* it is either absent (in the male) or represented by a false stigma (in the female). With regard to the principal veins, C extends to the wing apex, Sc lies some distance below and terminates at the nodus, R and M are fused basally and also Cu and A. The distal end of Sc is united with C by a thickened cross vein which forms a well defined "joint" or *nodus* on the wing margin. Recent work by Lameere, Tillyard (1928) and others has greatly modified previous interpretations of the venation. Study of the primitive fossil dragonfly *Kennedya* shows that, in all members of the order, vein M is represented by its convex division MA only (M_4 of most writers) while, of the cubitus, the concave branch Cu_2 alone persists.

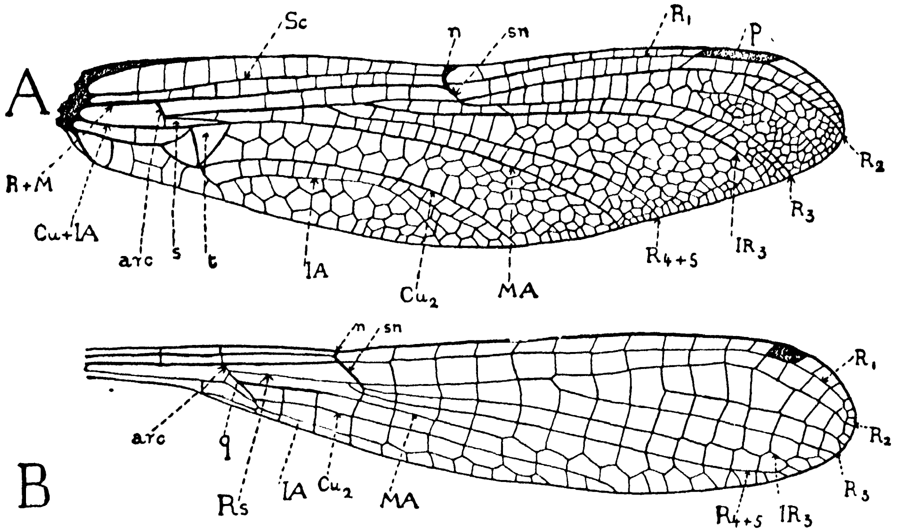

FIG. 332.—A, VENATION OF AN ANISOPTERID DRAGONFLY (CHIEF FEATURES ONLY). B, OF A ZYGOPTERID DRAGONFLY.

arc, arculus; IR_3, intercalated vein; *n*, nodus; *p*, pterostigma; *q*, quadrilateral; *s*, supra-triangle; *sn*, subnodus; *t*, triangle.

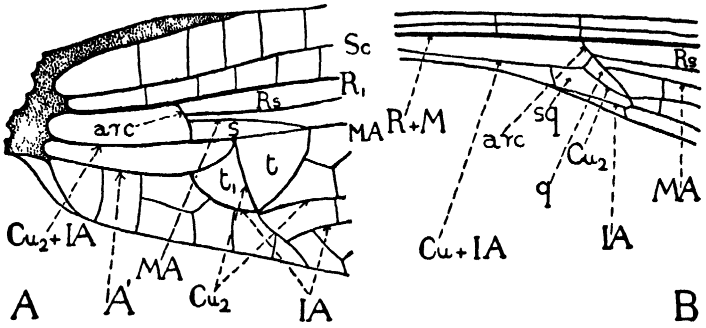

FIG. 333.—BASAL AREA OF FORE WING OF A, AN ANISOPTERID, AND B, A ZYGOPTERID.

A', secondary anal vein; *sq*, subquadrilateral; t_1, subtriangle. Other lettering as in Fig. 332.

The downwardly bent stem of Rs + M, together with the thickened cross-vein below it, form a characteristic feature—the *arculus*, which joins Cu. The discal cell is of great importance and, in the Zygoptera, it is often termed the *quadrilateral*, which is an area enclosed by MA above, Cu_2 below, the lower part of the arculus basally and a thickened cross-vein distally. In the Anisoptera this cell is subdivided into the *triangle* and *supra-triangle.* The former is a triangular area formed by Cu basally and by two thickened cross-veins costally and distally: the supra-triangle is the area from the arculus to the distal angle of the triangle.

The ABDOMEN (Fig. 334) is always greatly elongate in proportion to its breadth, and in extreme cases it is so attenuated as to be scarcely thicker than a stout bristle. Ten complete segments are evident, while according to Heymons vestiges of an 11th and of a 12th segment are also recognizable. The tergum of the 11th somite is represented by a median dorsal tubercle and its sternum by paired inferior tubercles. The 12th segment consists of three small processes immediately surrounding the anus:—a median dorsal *lamina supra-analis* and paired latero-ventral *laminæ infra-anales.* In the males of those Anisoptera which have angulated hind-wings a pair of lateral outgrowths or *auricles* are present on the 2nd tergum (Fig. 334C): in some cases they occur in the females also but are reduced in size. In all Odonata a pair of *supra-anal appendages* arise from the 10th tergum: they are well developed in the male but reduced or vestigial in the female. The males of the Anisoptera are also characterized by the presence of a *median inferior anal appendage* belonging to the 11th somite and situated above the anus. In the Zygoptera it is paired and situated below that aperture (Fig. 334D). During pairing, in all Odonata, the female is grasped by means of the anal appendages of the male, the superior pair establishing a firm grip in the region of the neck (among Anisoptera) or prothorax (among Zygoptera) while the inferior appendage is pressed down upon the occiput. In the Zygoptera the inferior pair is usually too short to reach the head.

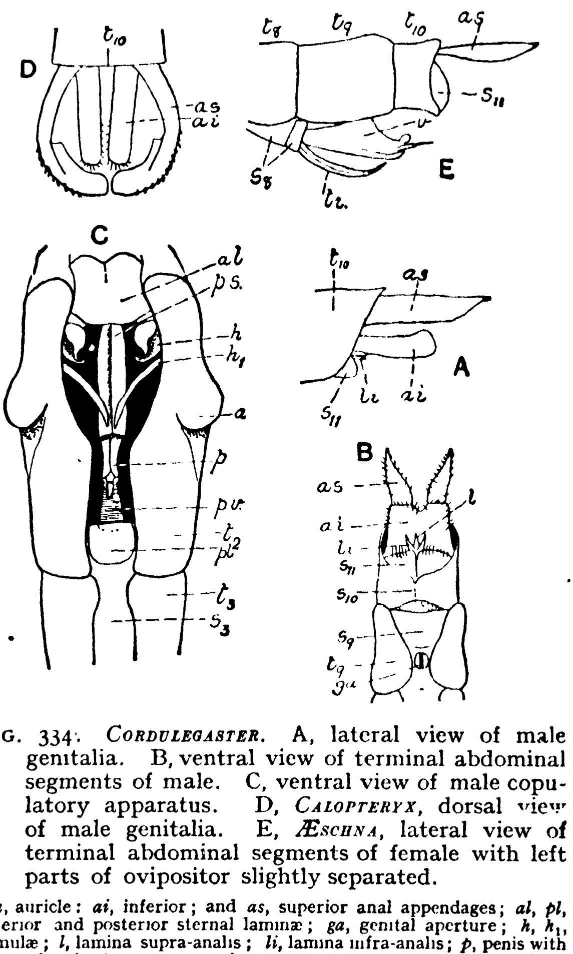

FIG. 334. *CORDULEGASTER.* A, lateral view of male genitalia. B, ventral view of terminal abdominal segments of male. C, ventral view of male copulatory apparatus. D, *CALOPTERYX*, dorsal view of male genitalia. E, *ÆSCHNA*, lateral view of terminal abdominal segments of female with left parts of ovipositor slightly separated.

a, auricle: *ai*, inferior; and *as*, superior anal appendages; *al*, *pl*, anterior and posterior sternal laminæ; *ga*, genital aperture; *h*, h_1, hamulæ; *l*, lamina supra-analis; *li*, lamina infra-analis; *p*, penis with *ps*, its sheath; *pv*, penis vesicule; *s*, sternum; *t*, tergum; *tr*, terebra; *v*, valve.

The copulatory organs of the male (Fig. 334C) are quite unique in the animal kingdom, being developed from the 2nd and 3rd abdominal sterna, whereas the true genital aperture opens on the 9th segment. On the 2nd sternum is a depression or *genital fossa* in which the copulatory organs are lodged and its walls are supported by a complex chitinous framework. The fossa communicates posteriorly with a small sac—the *penis vesicle* which is developed from the anterior portion of the 3rd sternum. The *penis* arises from this vesicle and, in the Anisoptera, it forms a complex jointed organ provided with an orifice on its convex surface. In the Zygoptera its only communication is with the body cavity and there is no distal aperture. One or two pairs of claspers or *hamuli* are associated with the penis and serve to guide and retain the ovipositor in position during copulation. The posterior pair of hamuli is universal but the anterior pair is only met with in the Æschnidæ. Great variation of structure is exhibited by the genitalia in various genera and for detailed information reference should be made to the works of Selys-Longchamps and Hagen (1858) and Thompson (1908). Owing to the wide separation of the copulatory organs from the genital aperture, the spermatozoa have to be transferred to the penis vesicle, prior to copulation. In the female the external genitalia consist typically of three pairs of ventral processes or gonapophyses which constitute the ovipositor (Fig. 334E). Among the Zygoptera the anterior and median gonapophyses are slender structures often adapted for cutting: these together form the terebra. The lateral gonapophyses or valves are broad lamellate organs each terminating in a hard pointed style which is probably tactile in function. Among the Anisoptera various stages in reduction of the ovipositor may be traced, which are correlated with different methods of oviposition.

Internal Anatomy.—Most of the internal organs are greatly elongated in conformity with the length of the body in these insects. The *alimentary canal* is an unconvoluted tube throughout its course. The œsophagus is long and slender, expanding into a crop at the commencement of the abdomen. A rudimentary gizzard is present but its armature of denticles is either very weak or absent. The mid-intestine is the largest division of the gut and extends through the greater part of the abdomen : it is devoid of enteric cœca and is followed by a very short hind-intestine. Attached to the latter are from 50 to 70 Malpighian tubes which unite in groups of five or six, each group discharging into the gut by means of a common conduit of extremely small calibre. Six longitudinal rectal papillæ are usually present. The *nervous system* is well developed and exhibits comparatively little concentration. The brain is transversely elongated and is characterized by the great development of the optic ganglia, which is in correlation with the large size of the eyes. The ventral nerve cord consists of three thoracic ganglia and seven evident ganglia (2nd to 8th) in the abdomen, the 1st abdominal ganglion being amalgamated with that of the metathorax. A well-developed sympathetic system is described by Brandt in *Libellula*. The circulatory system has not been studied in any detail but appears to be very similar to that of the nymph, with the exception that a ventral blood sinus is present in the imago in close relation with the main nerve cord. The tracheal system consists of three pairs of principal longitudinal trunks which give off segmental branches. It communicates with the exterior by means of ten pairs of spiracles situated on the last two thoracic and the first eight abdominal segments. The *male reproductive organs* consist of a pair of very elongate *testes* extending, in *Æschna*, from the 4th to the 8th abdominal segments: each organ is composed of a large number of spherical lobules in which the spermatozoa are developed. The vasa deferentia are rather short narrow tubes which enter a common duct just above the genital aperture. The common passage is dilated dorsally to form a conspicuous sperm-sac. The spermatozoa adhere in a radiating fashion forming rounded masses or sperm-capsules, each of the latter being apparently derived from a single lobule of the testis.

These capsules are somewhat mucilaginous externally and are adapted for transference from the ninth to the second segment, prior to copulation. The *female reproductive organs* are characterized by the great size and length of the ovaries which extend from the base of the abdomen down to the 7th segment. Each ovary is composed of a large number of longitudinally arranged panoistic ovarioles. The two oviducts are very short and open into a large pouch-like spermatheca in the 8th segment. A pair of accessory glands communicate by means of a common duct with the dorsal side of the spermatheca.

Structure and Biology of the Developmental Instars

Oviposition in dragonflies may be either endophytic or exophytic. In the latter case the eggs are rounded and are either dropped freely into the water or attached superficially to aquatic plants. This method is the rule among the Anisoptera, with the exception of certain Æschnidæ. In *Sympetrum* and *Tetragoneuria* the eggs are laid in gelatinous strings attached to submerged twigs. Endophytic oviposition is characteristic of the Zygoptera and the subfamilies Æschninæ and Petalurinæ of the Æschnidæ (Tillyard). Dragonflies adopting this method have elongate eggs which they insert by means of slits cut by the ovipositor in the stems and leaves of plants or other objects, near or beneath the water. In some cases the female (alone, or accompanied by the male) descends below the water-surface for the purpose.

Before the nymph emerges from the egg a peculiar pulsating organ or cephalic heart appears in the head of the developing insect. The pressure exerted by this vesicle is the immediate cause of hatching, since it forces open the lid-like anterior extremity of the egg. The newly hatched insect is known as the pro-nymph : at this stage it exhibits a more or less embryonic appearance, the whole body and appendages being invested by a delicate chitinous sheath. The pro-nymph is of extremely brief duration, lasting but a few seconds in *Anax* (Tillyard) and for two or three minutes in *Agrion* (Balfour Browne). At this stage the pulsations of the cephalic heart increase in frequency and the pressure generated by this organ also serves to rupture the pro-nymphal sheath. The insect which emerges is in its second instar : it is now a free nymph fully equipped for its future life. The nymphs of the Odonata are campodeiform and may be divided into two main types—the Anisopterid and the Zygopterid. In the former the body is terminated by three usually small processes, viz.—a median appendix dorsalis and a pair of lateral cerci : when closed they form a pyramid which conceals the anus (Fig. 335). Respiration takes place by means of concealed rectal tracheal gills. In the Zygopterid type the three terminal processes are greatly developed to form caudal gills, and rectal tracheal gills are wanting (Fig. 336). The nymphs are exclusively aquatic, living in various situations in fresh water. Many live hidden in sand or mud, etc., and are homogeneously coloured without any pattern. Those which live on the river bottom or among weed exhibit a cryptic pattern which tends to conceal them from enemies and prey. Certain species cling to rocks and tend to simulate the colour of the surface which they frequent. Dragonfly nymphs are also able to change their general coloration in accordance with differences in their environment. Without exception all the species are predaceous, feeding upon various forms of aquatic life, tbe nature of the food depending upon the age of the nymphs. When advanced in life they are particularly addicted to Ephemerid nymphs and Culicid larvæ as well as nymphs of their own and other species of Odonata. The larger Æschnine nymphs will also attack tadpoles and occasionally small fish. The number of instars that intervene between the egg and the imago varies in different species and also among individuals of the same species. It ranges between about eleven and fifteen and the whole nymphal period may be passed through within a year as in most Zygoptera, or occupy two years as in *Æschna*, or may even last from three to five years. The principal external changes involved during metamorphosis include an increase in the size of the compound eyes, and during the last few instars ocelli become evident: the antennal joints increase in number, and the wing-rudiments undergo certain changes with the result that the developing hind-wings overlap the anterior pair: the wing-bearing segments increase in size, and changes are evident in the caudal gills among the Zygoptera.

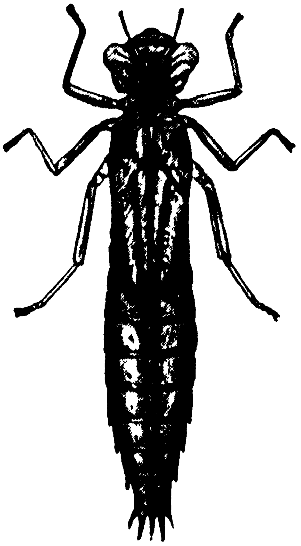

FIG. 335. NYMPH OF *BRACHYTRON PRATENSE*. × 1·6.

From a drawing by W. J. Lucas.

When the imago is approaching the time for emergence the nymph ceases to feed and appears tense and swollen. The thorax in particular becomes noticeably inflated and the wing-sheaths become sub-erect. The gills are no longer functional and at the same time the thoracic spiracles are brought into use, the nymph partially protruding itself from the water in order to breathe the atmosphere. When the internal changes are complete the nymph climbs up some suitable object out of the water and fixes its claws so firmly in position that the exuviæ remains tightly adherent to the support long after the imago has flown away. The nymph remains stationary and sooner or later the cuticle splits along the mid-dorsal line of the thorax, the fracture extending forwards to the head. The imago then withdraws its head and thorax through the opening, the legs and wings become freed, but the abdomen is not yet fully drawn out from the exuviæ. The insect usually hangs head downwards until the legs attain strength and freedom of movement. The withdrawal of the abdomen forms the final act, and the insect crawls away to rest until the wings and abdomen are fully extended (Fig. 206). A variable period elapses before the imaginal colour pattern is fully acquired and teneral forms, or individuals which have not yet developed their mature coloration, are very commonly observable on the wing.

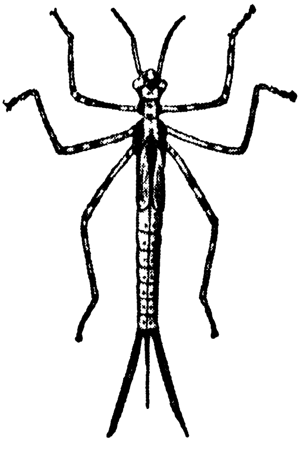

FIG. 336. NYMPH OF *CALOPTERYX SPLENDENS*. × 1·25.

From a drawing by W. J. Lucas.

The main difference between the head of the nymph and that of the imago is found in the labium. In the nymph this organ is modified for prehensile purposes and is known as the *mask* (Fig. 338) from the fact that it conceals the other mouth-parts. The prementum and postmentum are markedly lengthened, and there is a great freedom of movement between the two parts. The ligula is undivided and represented by a median lobe which is fused with the mentum. The labial palpi are modified to form lateral lobes, each of which carries on its outer side a movable hook. The nymph utilizes its mask entirely for the capture of prey (Fig. 337). In a position of rest the postmentum is reflexed between the bases of the legs with the prementum hinged upon it ventrally. When about to seize a victim the mask is thrown forward and extended with lightning rapidity and the prey impaled on the movable hooks.

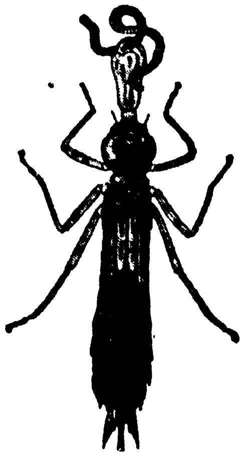
FIG. 337.—NYMPH OF *ANAX IMPERATOR* WITH MASK EXTENDED AND SEIZING PREY. × ·8

From a drawing by W. J. Lucas.

The prothorax in the nymph is always longer than in the imago: in advanced nymphs the meso- and meta-thorax are closely fused. The legs are considerably longer than those of the imago and the femoro-trochanteric articulation is modified to form a breaking joint. By a sudden contraction of the trochanteric muscles the intervening membrane can be ruptured, and the limb discarded should it be seized by a predatory insect. Ten segments are clearly recognizable in the abdomen and according to Heymons (1904) the 11th and 12th segments are also present in a much reduced condition (Fig. 339). The eleventh segment is represented dorsally by the base of the dorsal appendage (to be described below) and its sternum by the bases of the cerci. The twelfth tergum persists as the lamina supra-analis and the laminæ sub-anales represent the divided sternum of that segment. Three large appendages can be readily made out in the nymphs—a median dorsal appendage and two latero-ventral cerci: these structures form the caudal gills of the Zygoptera. From the fourth or fifth instar onwards a second set of appendages appears and gives rise to the imaginal genitalia. They consist, in both sexes, of a pair of small pointed structures (the cercoids of Heymons) lying above the cerci: the superior appendages of the male imago and the anal appendages of the female are derived from these organs. At the final metamorphosis the median dorsal appendage is cast off, but in male Anisoptera a small basal process persists as the inferior appendage of the adult. The cerci disappear except in males of the Zygoptera whose inferior appendages are developed within their bases.

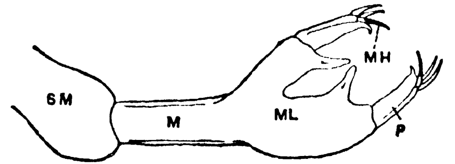

FIG. 338.—MASK OF NYMPH OF *CALOPTERYX*.

SM, postmentum; *M*, prementum; *ML*, median lobe; *P*, palp, *MH*, movable hook.

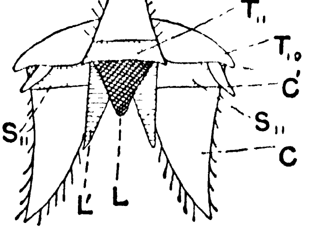

FIG. 339.—DIAGRAM OF THE ANAL APPENDAGES OF A DRAGONFLY NYMPH VIEWED FROM BEHIND WITH THE MEDIAN DORSAL APPENDAGE (D) LIFTED UPWARDS. BASED ON HEYMONS.

C, cercus; *C′*, cercoid; *L*, lamina supra-analis; *L′*, lamina infra-analis; S_{11}, 11th sternum; T_{10}, T_{11}, 10th and 11th terga.

The alimentary canal of the nymph (vide Sadones, 1896) differs from that of the imago in several features. The gizzard, for example, is a very highly specialized organ provided with internal denticle-bearing longitudinal ridges: the latter are either four or some multiple of four in number among different groups of the order. The mid-intestine is considerably shorter than in the imago, and the Malpighian tubes at first number only three but gradually increase at each instar until the full complement is acquired. The nervous system is more especially characterized by the presence of eight abdominal ganglia, the first centre in that series being quite distinct from the metathoracic ganglion although becoming fused with the latter in the imago. The circulatory system has been studied by Zwarsin (1911) in *Æschna*. The heart consists of eight chambers corresponding with the 2nd to 9th abdominal segments in which they lie: alary muscles are only present in relation with the two hindmost chambers. The respiratory system presents features of exceptional interest and has been investigated more particularly by Oustalet (1869), Sadones (1896) and Tillyard (1916). Spiracles are present on the meso- and meta-thorax but only the mesothoracic pair is well developed and is functional when the larva has occasion to leave the water. The metathoracic and abdominal spiracles are small and usually non-functional. Special respiratory organs in the form of tracheal gills are present in the nymphs of all dragonflies. In the Anisoptera they take the form of rectal gills which form an elaborate and beautiful apparatus known as the branchial basket. In most Zygoptera the respiratory organs are caudal gills, while in a few rare cases lateral abdominal gills are also present. These three types are treated separately below.

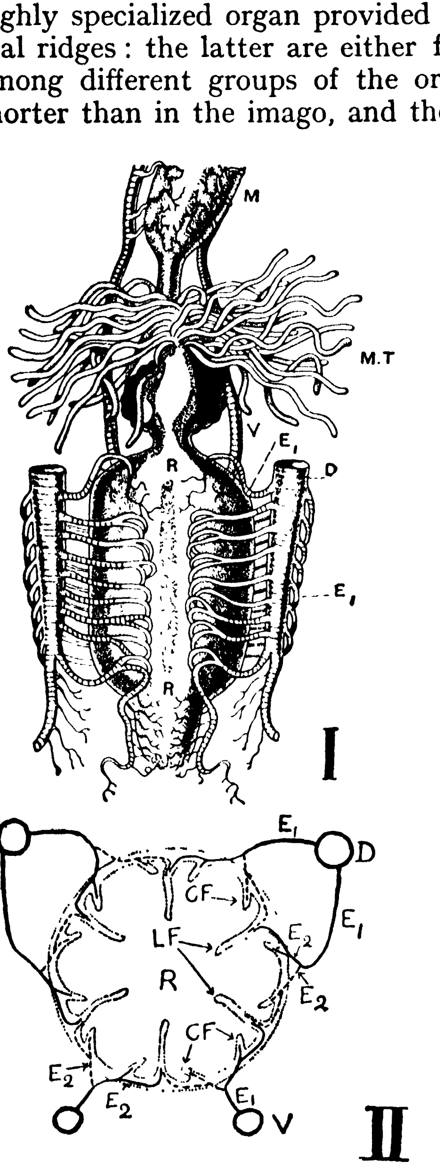

FIG. 340.—I. HIND-INTESTINE OF A NYMPH OF *ÆSCHNA* SHOWING TRACHEAL SUPPLY. AFTER OUSTALET. II. DIAGRAMMATIC TRANSVERSE SECTION OF THE RECTUM OF THE NYMPH OF *AUSTROGOMPHUS*. ADAPTED FROM TILLYARD.

CF, cross-fold; *D*, dorsal tracheal trunk; E_1 primary efferent trachea; E_2, secondary do.; *LF*, longitudinal fold; *M*, mid-intestine; *MT*, Malpighian tubes; *R*, rectum; *V*, visceral tracheal trunk.

(1) The BRANCHIAL BASKET.—This structure is formed by the expanded anterior two-thirds of the rectum, which assumes the form of a barrel-like chamber (Fig. 340). The gills are primarily developed as six longitudinal folds of the rectal wall and are homologous with the six rectal papillæ. They are covered with an extremely delicate cuticle and the underlying epithelial layer is modified to form a syncytial core which is penetrated by tracheoles. Water is alternately taken into the rectum and expelled and, in this manner,

the gills are kept aërated. The expulsion of the water, when forcible, also enables the nymph to propel itself forward by a series of jerks, which is its usual mode of progression. Six series of primary efferent tracheæ convey the oxygen, taken up by the gills from the water, to the main longitudinal trunks of the body. Each primary efferent trachea divides into two secondary efferents which give off a very large number of tracheoles to the gills. Each tracheole forms a complete loop within the gill, returning to the same secondary efferent from which it arose. The gill system may be either simplex or duplex in character (Fig. 341). In the *simplex system* there are six principal longitudinal gill folds supported right and left by a double series of cross folds. The simplex system is divisible into two types, the undulate and the papillate. In the undulate type the free edge of each gill-fold is undulated or wavy in character. This is the primary type of gill which persists throughout life in the more archaic groups (Cordulegasterinæ, Petalurinæ and in *Austrogomphus*). In most of the Gomphinæ all the gill folds are broken up into elongate filaments forming what is termed the papillate type. This specialization brings about greater respiratory efficiency since each filament is bathed on all sides by the water. The *duplex system* is a secondary development and differs in that the main longitudinal folds are either non-functional or wanting, the gills being entirely formed from the double series of cross-folds. Three main types in this system are recognizable and depend upon the form assumed by the gills. The implicate type occurs in the tribe Brachytronini of the subfamily Æschninæ. The gills resemble a series of obliquely placed concave tiles slightly overlapping one another. In the foliate type, which is found in the Æschnini, each gill is basally constricted and leaf-like in form. The lamellate type occurs in the family Libellulidæ: the gills appear as flat plates projecting into the cavity of the rectum and are attached by broad bases. For full details concerning the types of rectal gills and the differences in their tracheal supply reference should be made to an important paper by Tillyard (1916).

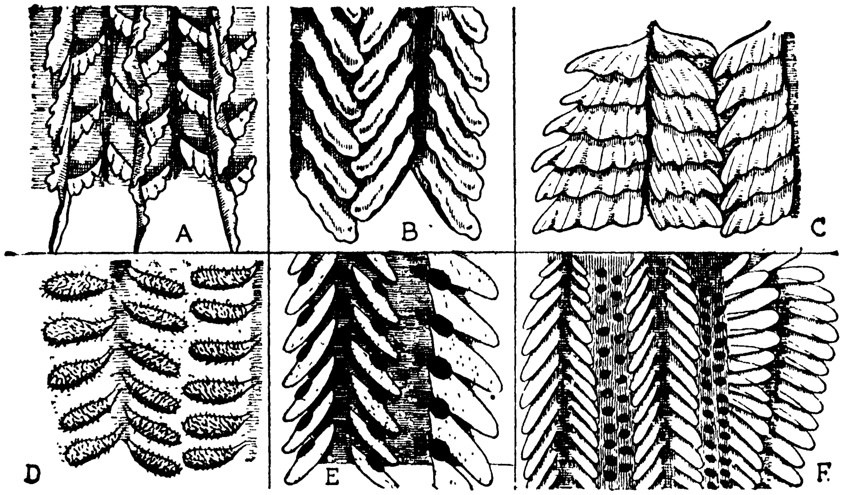

FIG. 341.—PORTIONS OF THE FRESHLY-OPENED BRANCHIAL BASKET, TO SHOW FORM OF GILLS. *A*, undulate simplex; *B*, implicate; *C*, foliate; *D*, papillo-foliate; *E*, *F*, lamellate. *After* Tillyard, *Biology of Dragonflies*.

(2) The CAUDAL GILLS.—Nearly all Zygopterid nymphs possess three external tracheal gills at the hinder extremity (Fig. 336). The median gill is dorsal and is developed from the appendix dorsalis, while the two lateral

gills are derived from the cerci. In the young nymph the caudal gills are filamentous and hairy, but they soon acquire a triquetral form (i.e. triangular in cross-section). The triquetral gill is retained throughout life in a few cases, as for example in the lateral gills of *Calopteryx*. In most instances it either becomes swollen (saccoid gill) or flattened (lamellate gill).

The problem of respiration in Zygopterous nymphs is reviewed by Calvert (1915) and is in need of fuller investigation. The caudal gills are evidently not the only respiratory organs and the amputation of these appendages does not lead to the death of the animal It would appear that the nymphs of this sub-order also use the rectum as an auxiliary respiratory chamber. The rectal papillæ, however, have no special tracheal supply and presumably function as blood gills: the latter are not to be confused with the rectal tracheal gills of Anisoptera. The general body-surface, certain of the spiracles and, in rare cases, the lateral abdominal gills (vide below) all contribute to satisfying the respiratory needs either in different stages or in different species of Zygoptera.

(3) The LATERAL ABDOMINAL GILLS.—These occur on either side of the 2nd to 7th or 8th abdominal segments in a few primitive genera of Calopterygidæ. They are attached towards the ventral surface and are filamentous in form. Possibly they are to be regarded as persistent true abdominal appendages.

Classification of Odonata

The Odonata are separable into two main sub-orders and five families, all of which are represented in the British Isles. The Anisoptera are strongly built, swiftly flying insects and include the larger members of the order. The Zygoptera are weak, slender-bodied insects with a poor capacity for flight and are usually smaller insects. The following classification is based upon that of Tillyard (1917).

Sub-order I. ANISOPTERA

Wings held open in repose: hind-wing always more or less broader near base than fore-wing. Eyes not separated by a space greater than their own diameter. Discal cell divided into triangle and super-triangle. Male with one inferior anal appendage. Nymphs with rectal tracheal gills.

FAM. 1. ÆSCHNIDÆ.—TRIANGLES VERY SIMILAR IN BOTH PAIRS OF WINGS, PLACED EQUALLY DISTANT FROM ARCULUS. ANTENODAL VEINLETS NOT PREDOMINANTLY COINCIDENT IN COSTAL AND SUBCOSTAL SERIES. LABIUM WITH A LARGE MEDIAN LOBE NOT OVERLAPPED BY LATERAL LOBES WHICH HAVE A MOVABLE HOOK. *Gomphus, Petalura, Cordulegaster, Æschna, Anax.*

FAM. 2. LIBELLULIDÆ.—TRIANGLES DISSIMILAR IN THE TWO PAIRS OF WINGS, NOT EQUALLY DISTANT FROM ARCULUS. ANTENODAL VEINLETS PREDOMINANTLY COINCIDENT IN COSTAL AND SUBCOSTAL SERIES. LABIUM WITH A SMALL MEDIAN LOBE OVERLAPPED BY LARGE LATERAL LOBES WHICH HAVE NO MOVABLE HOOK. *Cordulia, Libellula, Sympetrum, Leucorrinia, Trithemis.*

Sub-order II. ZYGOPTERA

Wings held closed over abdomen in repose: fore- and hind-wings closely alike with narrow bases. Eyes separated by a space greater than their dorsal diameter. Discal cell a simple quadrilateral. Male with two inferior anal appendages. Nymphs with caudal gills.

FAM 3. CALOPTERYGIDÆ.—WINGS SELDOM DISTINCTLY PETIOLATE, GENER-

ALLY COLOURED. ANTENODAL VEINLETS NUMEROUS: NODUS DISTANT FROM WING BASE: IR_3 ARISES FROM R_{2+3} FAR PROXIMALLY TO NODUS. *Calopteryx, Rhinocypha, Diphlebia.*

FAM. 4. LESTIDÆ.—WINGS DISTINCTLY PETIOLATE, RARELY COLOURED. ANTENODAL VEINLETS VARIABLE IN NUMBER: NODUS VARIABLE IN POSITION: IR_3 FUSED WITH R_3 FOR SOME DISTANCE, LEAVING IT *via* AN OBLIQUE VEIN: VERY LITTLE ARRANGEMENT OF CROSS-VEINS IN TRANSVERSE SERIES. *Lestes, Synlestes.*

FAM. 5. AGRIONIDÆ.—WINGS DISTINCTLY PETIOLATE, RARELY COLOURED. ANTENODAL VEINLETS TWO: NODUS RARELY MORE THAN $\frac{1}{8}$ OF WING LENGTH FROM WING BASE: IR_3 GENERALLY ARISING AT SUBNODUS: CROSS-VEINS ARRANGED IN TRANSVERSE SERIES. *Agrion, Platycnemis, Ischnura, Pyrrhosoma, Enallagma.*

Sub-order III. ANISOZYGOPTERA.

This sub-order was established by Handlirsch for a group of Liassic Odonata which appear to have combined the characters of sub-orders I and II. At the present day it is only represented by the genus *Epiophlebia* (Fig. 327) which has been referred to the family Lestidæ. The genus is known from a single species of imago from Japan and a species of nymph from India. The imago has the Zygopterid venation and the body-form of the Anisoptera, while the nymph has the general facies, labial mask and anal appendages of the latter sub-order (vide Tillyard, *Rec. Ind. Mus.* 22).

Literature on Odonata

A good bibliography of the order is given by Tillyard (1917) and only a selection of works is enumerated below.

BALFOUR-BROWNE, 1909.–The Life-History of the Agrionid Dragonfly. *Proc. Zool. Soc.* **CALVERT, 1911-15.**–Studies in Costa Rican Odonata. I–VII. *Ent. News,* 22–26. **HEYMONS, 1904.**–Die Hinterleibesanhänge der Libellen und ihrer Larven. *Ann. Hofmus. Wien* 19. **LUCAS, 1900.**–British Dragonflies. London. —— **1930.**–The Aquatic Stage of British Dragonflies. London; *Ray Soc.* **NEEDHAM and HEYWOOD, 1929.**–Dragonflies of N. America. Springfield, Mass. **OUSTALET, 1869.**–Note sur la Respiration chez les Nymphes des Libellules. *Ann. Sci. Nat. Zool.* ser. 5, 11. **RIS, 1909.**–Odonata in " Süsswasserfauna Deutschlands." Jena. **SADONES, 1896.**–L'appareil digestif et respiration larvaire des Odonates. *La Cellule,* 11. **SELYS-LONGCHAMPS and HAGEN, 1858.**–Monographie des Gomphines. Brussels. **THOMPSON, O. S., 1908.**–Appendages of the second abdominal segment of male dragonflies. *N.Y. State Mus. Bull.* 124. **TILLYARD, 1916.**–On the Rectal Breathing Apparatus of Anisopterid Larvæ. *Journ. Linn. Soc. Zool.* 33. —— **1917.**–The Biology of Dragonflies. Cambridge. —— **1928.**–The Evolution of the Order Odonata. Part I. Introduction, etc. *Rec. Indian Mus.* 30. **ZAWARSIN, 1911-12.**–Histologische Studien über Insekten. 1. Das Herz der Æschnalarven. *Zeit. wiss. Zool.* 97. 2. Das sensibel Nervensystem der *Æschna*-larva. *Ibid.* 100.

Order 13. THYSANOPTERA (Physopoda : Thrips)

SMALL OR MINUTE SLENDER-BODIED INSECTS WITH SHORT 6- TO 9-JOINTED ANTENNÆ AND ASYMMETRICAL PIERCING MOUTH-PARTS: MAXILLARY AND LABIAL PALPI PRESENT. PROTHORAX WELL DEVELOPED, FREE: TARSI 1- OR 2-JOINTED, EACH WITH A TERMINAL PROTRUSIBLE VESICLE. WINGS WHEN PRESENT VERY NARROW WITH GREATLY REDUCED VENATION AND LONG MARGINAL SETÆ. CERCI ABSENT. METAMORPHOSIS ACCOMPANIED BY AN INCIPIENT PUPAL INSTAR.

The insects comprised in this order are commonly known as ' thrips." The majority vary in length from $\frac{1}{50}$ to $\frac{1}{3}$ of an inch, the smaller forms being by far the most prevalent. They are mostly yellow, yellowish-brown or black in colour and are found among all kinds of growing vegetation, both on the flowers and about the foliage: others frequent moist decaying plant remains, particularly wood and fungi. Some species are predaceous, or at least occasionally so, and suck the body-fluids of aphids and small acari. When disturbed different species exhibit certain differences of movement: some crawl in a leisurely fashion, others run quickly or leap, and a large number are able to fly but they often do not readily resort to this means of locomotion. Many exhibit the habit of curving the apex of the abdomen upwards and, in the case of winged individuals, this movement is generally preparatory to flight: it appears to be for the purpose of drawing the lateral comb-like setæ of the abdomen through the marginal fringes of the wings. The latter organs when in repose are laid in a more or less parallel manner along the back.

The vast majority of species derive their nutriment by penetrating the living tissues of plants by means of their piercing mouth-parts, and imbibing the sap. It is, therefore, not surprising that certain members of the order are recognized by economic entomologists as pests, especially the pear thrips (*Tæniothrips inconsequens* Uzel [*pyri* Dan.]), the onion thrips (*Thrips tabaci*), the grass thrips (*Anaphothrips striatus*), the greenhouse thrips (*Heliothrips hæmorrhoidalis*) and several others. In addition to the particular plants with which their names are associated, these, and other species, affect a wide range of hosts, and several are polyphagous. On the other hand, a number of species have so far only been obtained from single plant species. The primary injury to vegetation is caused by the extraction of the sap and, when severe, a whole crop may be ruined. The effects of the injuries are very variable in different cases; in apple blossoms, for example, thrips have been known to prevent the formation of fruit, and Hewitt has found that when *A. striatus* feeds upon the spikelets of oats it produces sterility (vide *Journ. Econ. Ent.* 7). It is true, however, that thrips play a part in the fertilizing of beet, and many other plants, but their value in this direction does not compensate for their injurious feeding habits. Some species, notably the corn thrips (*Limothrips cerealium*), are well known to be capable of sustained flight and migration: in such instances they fly in large numbers, particularly during sultry weather.

Parthenogenesis is of frequent occurrence throughout the order, and in several species (*H. hæmorrhoidalis*, *T. inconsequens*, etc.) males are either unknown or extremely rare: in others the eggs are capable of developing parthenogenetically, although males are quite common.

Approximately 1,500 species of the order have been described, and about one hundred have been found in the British Isles. The most important general works on the order are those of Uzel (1895) and Priesner (1928). For the British forms reference should be made to the writings of Haliday (*Ent. Month. Mag.* 1836–37) and Bagnall (*Journ. Econ. Biol.* 1911–13, and other papers).

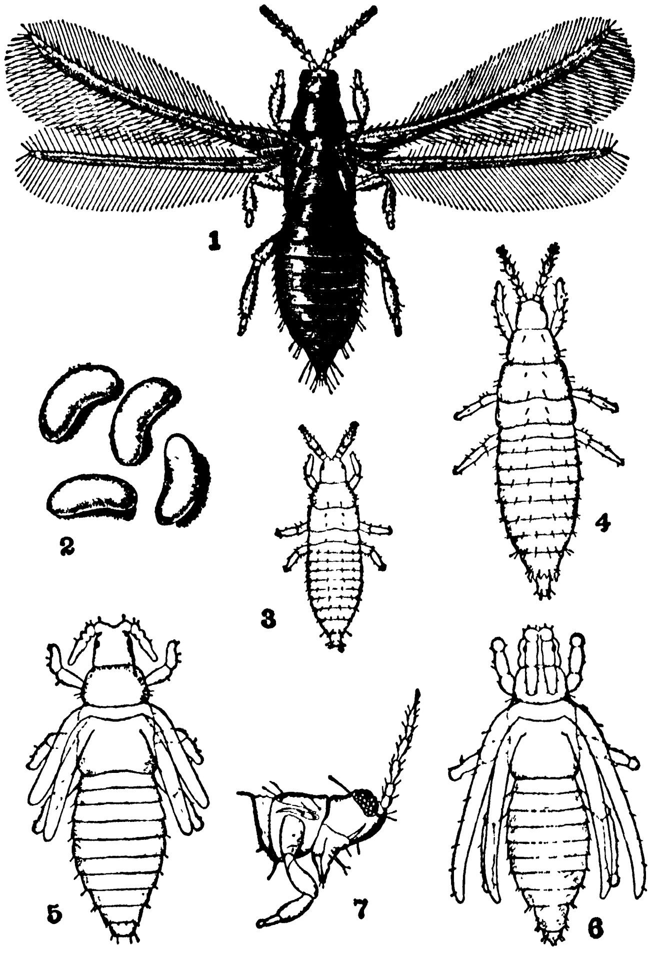

FIG. 342.—THE PEAR THRIPS (*TÆNIOTHRIPS INCONSEQUENS* UZEL: *PYRI* DAN).

1, Imago; 2, eggs; 3, first instar nymph; 4, fully-grown nymph; 5, pre-pupa; 6, pupa; 7, lateral view of head of imago. Reduced from Foster and Jones. *U.S. Dept. Agric. Bull.* 173.

External Anatomy.—In their general structure the Thysanoptera are more closely related to the Hemiptera-Homoptera than to any other order of insects. The head is generally somewhat quadrangular in form with a pair of small but prominent compound eyes: the facets of the latter are relatively large and convex, assuming a rounded instead of the usual hexagonal form. Three ocelli are commonly present on the vertex. Nearly all the head sclerites are intimately fused, almost all traces of sutures being lost. The antennæ are 6- to 9-jointed, and are inserted close together in a very forward position. The mouth-parts are adapted for piercing and suction, certain of the organs being modified as stylets which are enclosed in a short cone, or rostrum, projecting downwards from the ventral surface of the head (Fig. 343). The structure of the trophi has received attention from a number of investigators, including Muir and Kershaw (1911), Borden (1915), Peterson (1915) and Reinje (1926). Their small size and asymmetrical form render them difficult to study and, consequently, a good deal of difference of opinion exists with regard to the homologies of the stylets. The mouth-cone is formed by the labrum and clypeus above, and the labium below, while the actual piercing organs are protruded through the short tubular base thus formed. Among the Terebrantia the mandibles of the two sides are totally unlike: the left organ is a strong chitinized stylet while the right one is reduced to a vestigial condition. The maxillæ consist of a pair of palpus-bearing plates with associated stylets. The plates may be either symmetrical or unlike and they form the side walls of the mouth-cone already alluded to. The palpi are composed of a variable number of joints which range from 2 to 8 among different genera. Each stylet consists of a small basal piece articulating with the palpus-bearing plate of its side, and a long piercing organ which is usually divided into a proximal and a distal element. The labium forms the trough-like floor of the mouth-cone and is divisible into a mentum and submentum. The membranous apex of the mentum is more or less bilobed and carries a pair of short labial palpi which are 1- to 4-jointed. Among the Tubulifera certain differences in the mouth-parts are noticeable. The unpaired stylet articulates with the palpus-bearing plate of its side; the two paired stylets are very long and have acquired separate, and more posterior, articulations with the head capsule. These features have led Muir and Kershaw to regard the unpaired stylet as the maxilla, and the paired stylets as mandibles. Peterson, on the other hand, maintains that their homologies are the same as in the Terebrantia, basing his conclusions upon comparative studies of nymphs and adults of the two sub-orders. The connection of the mandible with the palpus-bearing plate of its side he regards as being secondary, since it is not present in the nymphal stage.

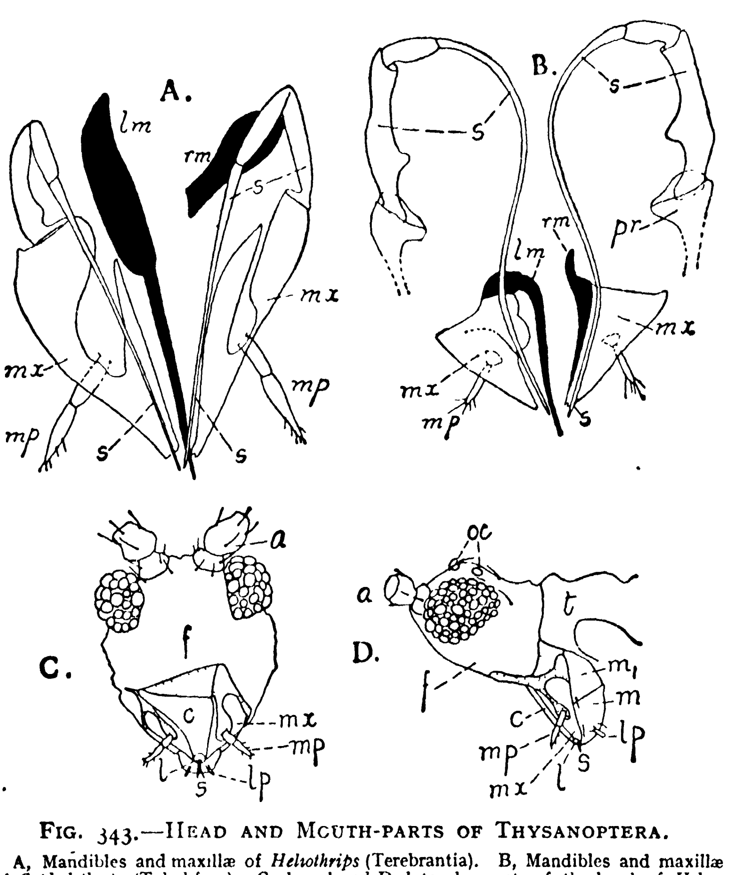

FIG. 343.—HEAD AND MOUTH-PARTS OF THYSANOPTERA.

A, Mandibles and maxillæ of *Heliothrips* (Terebrantia). B, Mandibles and maxillæ of *Cephalothrips* (Tubulifera). C, dorsal and D, lateral aspects of the head of *Heliothrips*. *a*, base of antenna; *c*, clypeus; *f*, frons; *l*, labrum; *lm*, left mandible; *lp*, labial palp; *m*, mentum; m_1, submentum; *mp*, maxillary palp; *mx*, maxillary plate; *oc*, ocelli; *pr*, internal process of head; *rm*, right mandible; *s*, maxillary stylet; *t*, thorax. Adapted from Peterson.

When a thrips feeds the apex of the mouth-cone is applied to the surface of the plant, and the stylets are driven into the tissues. The laceration of the latter causes a minute wound through which the sap escapes. The apex of the mouth-cone is applied to the puncture, and the juices of the plant are pumped up into the gut by means of the action of the pharyngeal muscles.

The prothorax is free and distinct, with a broad tergum, while the meso- and meta-thorax are compactly united. The legs are composed of the usual parts and only the tarsi present special features. The latter are 1- or 2-jointed, and the claws may be either single or paired. A remarkable protrusible vesicle is associated with the extremity of the tarsus, and it is to the presence of this organ the alternative ordinal name Physopoda is due. When at rest, the vesicle is retracted and invisible, but when the insect is walking it appears to be exserted by means of blood pressure. These organs are present in both nymphs and imagines and they enable their possessors to walk upon almost any kind of surface. The wings are membranous, very narrow, and strap-shaped: they have very few or no veins, and only rarely possess cross-veins. They are fringed with long setæ and some species bear spines along the veins or along the former courses of the latter. The wings of a side are interlocked by means of several hooked spines near the base of the hind-wing which engage a membranous fold on the anal area of the fore-wing. The imagines of many species exhibit striking variations in the degree of development of the wings. The adults of a single species (*Chirothrips manicatus* Hal.) may have fully developed wings, reduced functionless wings, or be completely apterous. In other species both sexes may be winged or one winged and the other apterous: one or both sexes may be brachypterous or both may be wingless. When brachypterous forms occur among normally winged individuals the phenomenon is especially evident towards autumn.

The abdomen is elongate, tapering posteriorly, and is composed of ten segments. In the Terebrantia there is a conspicuous serrated ovipositor projecting from the ventral surface between the eighth and ninth abdominal segments, and formed by two pairs of gonapophyses. Among the Tubulifera an ovipositor is wanting and the terminal segment is tubular.

Internal Anatomy.—Most of what is known concerning the internal structure of Thysanoptera is due to Jordan (1888) and Uzel (1895). The digestive system is characterized by a chitinized sucking pharynx provided with radial muscles, an extensive mid-intestine and four Malpighian tubes. The mid-intestine forms the largest portion of the alimentary canal and is divided into a capacious anterior chamber followed by a tubular coiled posterior region. The hind intestine forms a straight passage to the anus. Two pairs of *salivary glands* are commonly present and are located in the thorax and abdomen (vide Peterson, 1915): their ducts unite to form a common canal opening at the apex of the mouth-cone. According to Uzel three pairs of salivary glands are found in the thorax of *Trichothrips*. The *nervous system* is highly concentrated: the brain is well developed. the sub-œsophageal and prothoracic ganglia are fused while the meso- and meta-thoracic ganglia remain separate. A median nerve cord passes down the abdomen, but the ganglia have shifted forward and are concentrated into a single centre which is located in the first segment of that region. The *circulatory organ* consists of a very short contractile heart lying in the eighth abdominal segment and continued forwards as a long aorta. In the *female reproductive* organs the ovaries each consist of four short panoistic ovarioles: a receptaculum seminis is present together with small accessory glands. The *male reproductive organs* consist of a pair of fusiform testes which communicate by means of rather short vasa deferentia with an ejaculatory duct. The latter is somewhat swollen at its forward extremity, forming an ampulla-like enlargement. At this point it receives the ducts of one or two pairs of relatively large accessory glands which considerably exceed the testes in size. The *tracheal system* is well developed and usually opens to the exterior by means of three or four pairs of spiracles. One pair is located near the anterior angles of the mesothorax and there are also pairs on the 1st and 8th abdominal segments : a 4th pair is present in the Tubulifera and many of the Terebrantia, situated on the metathorax just behind the attachment of the hind-wings.

Life-history and Metamorphoses (Fig. 342).—The eggs of the Terebrantia are more or less reniform, while those of the Tubulifera are commonly elongate-oval. In the first-mentioned sub-order the female cuts a slit with her saw-like ovipositor, laying the eggs singly in the tissues of the host plant. The Tubulifera lay their eggs externally, either singly or in groups, upon leaves, stems, under bark, etc. The newly hatched nymphs resemble the imagines in their general facies and their method of feeding is also similar. There are generally four instars before the adult condition is reached. After the second ecdysis the nymphs develop wing-pads and assume what is frequently termed the prepupal instar. As a rule they conceal themselves among debris or enter the ground prior to undergoing this change, but in *Heliothrips hæmorrhoidalis* the transformation takes place on the underside of the leaves of the food plant. During the prepupal stage the insect often manifests considerable activity. In the case of those species which transform in the soil the prepupa is quiescent but will crawl about when removed from its earthen cell. The prepupa may be distinguished from the next instar or pupa by the antennæ remaining free and not being reflected over the head and pronotum : the wing pads are shorter, the compound eyes are still small and ocelli are wanting. After a comparatively short period spent in this stage the insect undergoes its third ecdysis and transforms into a pupa. This instar is of a variable, and often lengthy, duration among different species. Unless disturbed the pupa remains quiescent, but upon being roused it is capable of slowly crawling about. It is to be regarded as a resting nymphal stage exhibiting a definite approach towards the true pupa of the Endopterygota. No nourishment is taken during the prepupal and pupal instars. The number of generations passed through in the year differs in various species : many, such as *Tæniothrips inconsequens*, are univoltine, while on the other hand *Heliothrips fasciatus* is known to have 7 to 9 generations in a season in the United States. Hibernation may take place in the nymphal, pupal, or imaginal stage.

Classification.—In the following classification, after Karny (1921) and Priesner (1928), European families are indicated thus *.

Suborder I. **Terebrantia.** Ovipositor saw-like, apex of abdomen conical in female, bluntly rounded in male ; fore-wings with at least one longitudinal vein reaching to the apex.

1 (2).—Antennæ 9-jointed ; fore-wings broad with rounded apices ; ovipositor curved upwards ; body not flattened. **Æolothripidæ.***

2 (1).—Antennæ 6- to 10-jointed ; fore-wings narrow with apices more pointed ; ovipositor curved downwards ; body more or less flattened.

3 (8).—Prothorax without sutures ; wing surface pubescent.

4 (7).—Antennæ 9- or 10-jointed without a terminal style.

5 (6).—Third antennal joint cylindrical, not conical. **Hemithripidæ.**

6 (5).—Third and fourth antennal joints enlarged, conical without sense cones rarely with a sensory band at apex ; fore tarsus with claw-like appendage at base of 2nd joint. **Heterothripidæ.**

7 (4).—Antennæ 6- to 8-jointed, usually with a 1- or 2-jointed apical style; 3rd and 4th joints not conical, with sense cones; fore tarsus never with claw-like appendage at base of 2nd joint. **Thripidæ.***

8 (3).—Prothorax with longitudinal dorsal sutures; wing surface smooth; antennæ moniliform, 8-jointed without apical style, joints 3 and 4 without sense cones, each with a tympanum-like sense area on apex. Abdomen blunt; ovipositor very weak. **Merothripidæ.**

Suborder II. **Tubulifera.** Ovipositor absent; apex of abdomen in both sexes usually tubular; fore-wings with venation almost absent.

1 (12).—Maxillary palpi 2-jointed; antennæ 8-jointed, seldom 7-jointed; middle coxæ wider apart than fore or hind pairs; 9th abdominal segment not or rarely longer than 8th; terminal abdominal setæ seldom much longer than the tube.

2 (3).—Last abdominal segment not tubular, greatly swollen, parabolic in outline from above; 2nd to 9th abdominal terga transversely linear. **Pygothripidæ.**

3 (2).—Last abdominal segment slender, cylindrical or tubular, comprising the tube; 2nd to 9th abdominal terga not transversely linear.

4 (11).—Eighth abdominal segment without peg-like projections on hind margin.

5 (10).—Tube much shorter than remaining abdominal segments taken together.

6 (7).—Third antennal joint with a distal ring of very prominent sensory rods. **Ecacanthothripidæ.**

7 (6).—Sensory rods on 3rd antennal segment not stronger developed than on other segments.

8 (9).—Antennal sense cones extraordinary long and sharp. Eyes unusually large, touching each other; mouth cone sharply pointed. **Eupathithripidæ.**

9 (8).—Antennal sense cones not unusually developed; eyes seldom touching each other. **Phloeothripidæ.***

10 (5).—Tube about as long as remaining abdominal segments taken together. **Hystricothripidæ.***

11 (4).—Eighth abdominal segment with long peg-like projections on posterior margin. Antennæ and tube unusually short and thick. **Chirothripoididæ.**

12 (1).—Maxillary palp 1-jointed; antennæ 4- to 7-jointed; hind coxæ farther apart than remaining pairs; 9th abdominal segment longer than 8th; terminal abdominal setæ markedly longer than the tube. **Urothripidæ.***

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Order 14. HEMIPTERA (Rhynchota: Plant Bugs, etc.).

TWO PAIRS OF WINGS USUALLY PRESENT; THE ANTERIOR PAIR MOST OFTEN OF HARDER CONSISTENCY THAN THE POSTERIOR PAIR, EITHER UNIFORMLY SO (HOMOPTERA) OR WITH THE APICAL PORTION MORE MEMBRANOUS THAN THE REMAINDER (HETEROPTERA). MOUTH-PARTS PIERCING AND SUCTORIAL, PALPI ATROPHIED; THE LABIUM IN THE FORM OF A DORSALLY GROOVED SHEATH RECEIVING TWO PAIRS OF BRISTLE-LIKE STYLETS. METAMORPHOSIS USUALLY GRADUAL, RARELY COMPLETE.

The Hemiptera or Bugs are most easily recognized by the form of the mouth-parts. They are, without exception, sucking insects, and this habit, along with the general structure of the mouth-parts, is retained throughout life. The wings present a greater variation in structure than in any other order of insects, and for this reason no general definition is sufficiently comprehensive to include them all.

As Sharp observes, probably no other order of insects is so directly concerned with the welfare of man on account of the vast amount of direct, and indirect, injury its members entail to vegetation. Among the most destructive species are the Cotton Stainers (*Dysdercus*), the Chinch-bug (*Blissus leucopterus*), Tea Blight (*Helopeltis*), Leaf-hoppers (Jassidæ and related families), White Flies (Aleyrodidæ), Plant Lice (Aphididæ), and the Scale Insects and Mealy Bugs (Coccidæ). Certain Homoptera act as vectors transferring the viruses of such diseases as "mosaic," "leaf-roll," "yellows," &c., from plant to plant by means of their piercing mouth-parts. Aphides are the most important in this respect and *Myzus persicæ* alone is known to be able to carry the viruses of fourteen separate plant diseases including mosaic of potato, sugar-cane and sugar-beet and leaf-roll of potato. Jassidæ are also concerned with the transmission of aster "yellows," "curly-top" of sugar-beet and "streak" of maize.

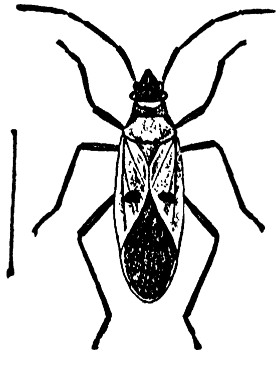

FIG. 344. — *DYSDERCUS CINGULATUS*.

After Distant in *Fauna of British India*.

An all-important factor bearing upon the devastation entailed by Hemiptera is the extraordinarily rapid rate of reproduction found in many members of the sub-order Homoptera. The calculations of Reaumur and Huxley regarding the fecundity of parthenogenetic aphides are well known. Buckton, however, regards their conclusions as greatly underestimated, and showed that the progeny of a single aphid at the end of 300 days—if all the members survived—would be the 15th power of 210! With regard to leaf-hoppers Perkins, on the supposition that each hopper lays 50 eggs (and the sexes are about equal), calculates that if there are six generations in the year the undisturbed progeny of one female would amount, at the end of twelve months, to very little less than 500,000,000.

Among certain Heteroptera a propensity for animal food has been acquired, particularly in the predaceous family Reduviidæ and in most Cryptocerata. The Cimicidæ, Polyctenidæ, and the Reduviid genus *Triatoma* are active blood-suckers of mammals or birds, the habit being prevalent in both sexes.

Hemiptera afford many instances of resemblance to insects of their own and other orders. Certain of the ant-like forms are very remarkable ; thus the Coreid *Dulichius inflatus* Kirby (brachypterous form) closely resembles and associates with the ant *Polyrachis spiniger*, and is furnished with pronotal and other spines, rather similar to those possessed by the ant. Another Coreid, *Alydus calcaratus* L., is often found in England in company with *Formica rufa* and other ants, which its nymph closely resembles. Further cases of resemblance to insects pertaining to other orders are met with in the Reduviidæ.

Aquatic Hemiptera afford excellent examples of the relation of structural modifications to differences of environment, particularly with regard to locomotion and respiration (vide Bueno, 1916). In the surface dwellers (Hydrometridæ) the adaptations are less pronounced, the antennæ free and unconcealed, and the legs not highly modified. These insects are clothed with velvety pile to prevent wetting, and respiratory devices are but little complicated. The Cryptocerata, on the other hand, have the antennæ concealed, the long antennæ of above-water forms obstructing the freedom of motion of submerged insects. The legs are highly adapted for purposes of swimming and respiratory modifications are complex.

External Anatomy

The Head.—The head (vide Muir and Kershaw, 1911, 1911A) is very variable both in form and in the inclination of its longitudinal axis. In almost all cases the sclerites are compactly fused (Fig. 345), only two principal dorsal

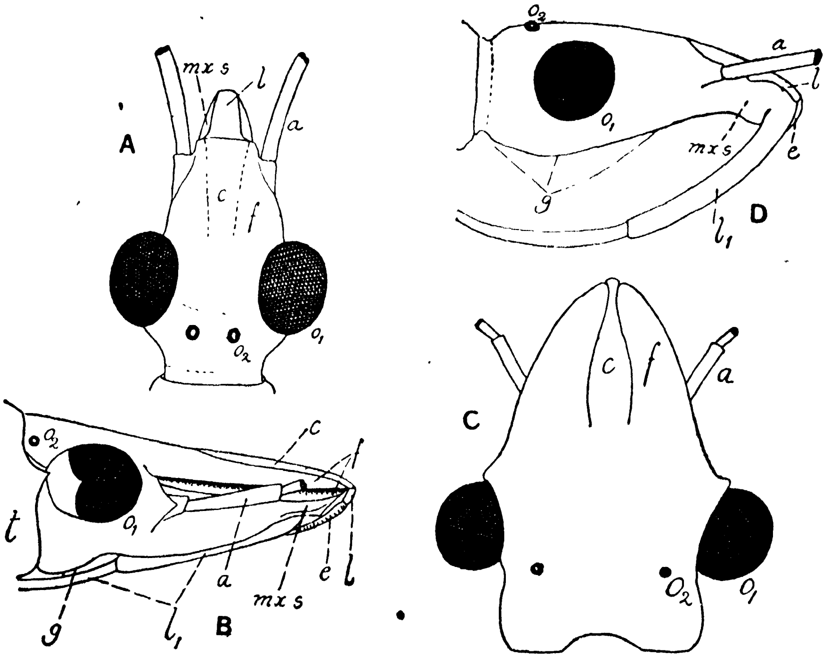

Fig. 345.—A and C, Dorsal Aspects of the Head of a Reduviid and a Pentatomid respectively : D and B, The Same viewed Laterally.

a, base of antenna ; *c*, clypeus ; *e*, epipharynx ; *f*, frontal process ; *g*, gula ; *l*, labrum ; l_1, labium (rostrum) ; *mx.s* maxillary sclerite ; o_1, compound eye ; o_2, ocellus ; *t*, prothorax.

plates—the epicranium and clypeus—being recognizable owing to the fusion of the frons with the former. In Psyllidæ however the frons is evident as a separate narrow sclerite carrying the median ocellus; the expression "frons" is frequently used in descriptive works dealing with the Auchenorhyncha, although this region can only be regarded as a conventional area, not definitely marked off from the epicranium. The frons, clypeus, and labrum of many systematists are, in a number of families, the clypeus, labrum and epipharynx respectively. The loræ are two curved plates evident in leaf-hoppers between the clypeus and genæ, and are lateral developments of the former. The labrum is rather variable in form and not always clearly separated from the epipharynx; the latter organ is narrow and acuminate. Ocelli are usually present and frequently two in number (Heteroptera, and most Auchenorhyncha); three are present in Cicadidæ, and many Sternorhyncha. They are wanting in Pyrrocoridæ, Cimicidæ and species of *Typhlocyba*, etc. In addition to compound eyes, ocular tubercles or supplementary eyes are present in close relation to the former in *Livia* and many aphides. The antennæ have few joints, frequently only four or five; their maximum number is attained in the Sternorhyncha, where 10 joints are found in Psyllids and 25 in the males of a few Coccids.

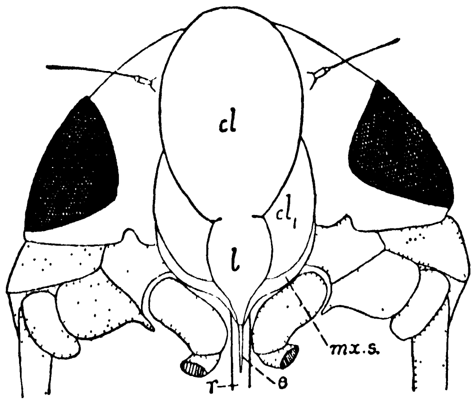

FIG. 346.—VENTRAL ASPECT OF THE HEAD OF A CERCOPID WITH ADJACENT THORACIC SCLERITES (DOTTED).

cl, clypeus; cl_1, lora; *e*, epipharynx; *l*, labrum; *mx.s*, maxillary sclerite; *r*, rostrum.

The **Mouth-parts** (Fig. 347).—These organs in the different families are very alike in general structure, the similarity being correlated with the uniform nature of the feeding habits throughout the order. They are exclusively adapted for piercing and suction, the mandibles and maxillæ being modified to form slender bristle-like stylets which rest in the grooved labium. The embryological studies of Heymons (1899), and Muir and Kershaw (1911, 1912), have demonstrated that the mandibles and maxillæ develop quite normally from the first two pairs of post-oral embryonic appendages. They subsequently become sunk to some extent within the head, and enclosed at their bases in pockets whose lining is continuous with the general integument. Both pairs of stylets are hollow seta-like structures, capable of limited protrusion and retraction by means of muscular action. In many Homoptera the stylets are extremely long and, in some cases, greatly exceed the total length of the insect. In these instances they are capable of being looped or coiled upon themselves, and withdrawn into a backwardly directed pocket connected with the channel of the labium. This pocket in Coccidæ (Fig. 379A) is lined by thin membrane, and is situated between the central nervous system and the ventral body-wall.

The mandibular stylets form the anterior (outer) pair and, although usually free, may be closely interlocked with the maxillæ as in *Lygus*: at their apices they are usually serrated. The posterior (inner) pair of stylets constitute part of the maxillæ: the embryonic rudiments of the latter become bi-segmented at an early stage, and the basal joint thus formed gives rise to the maxillary sclerite or plate, and the distal joint to the maxillary stylet. The swollen basal portion, or maxillary sclerite, is probably to be regarded as the undifferentiated cardo and stipes, which subsequently became amalgamated with the head capsule, while the stylet itself is to be looked upon as the homologue of a maxillary lobe. Maxillary palpi are wanting, except as vestigial organs, which occur in certain Hydrometridæ, while in some Tingidæ there are small processes which have been regarded as pertaining to the same category. Each maxillary stylet tapers to a fine point and is grooved along its inner aspect: the groove is divided into two parallel channels by means of a longitudinal ridge which traverses the length of stylet. Seen in cross section, the latter is shaped like a **W**, and the pair of stylets, by the approximation of their channels, form two extremely fine tubes. The dorsal one functions as the suction canal and communicates with the pharyngeal duct: the ventral tube is the ejection canal and receives the saliva discharged through the salivary duct. Within the head the maxillary stylets diverge towards their bases, but externally they are closely interlocked, and appear as a single structure, as in *Anasa* (Tower), and *Psylla* (Grove); or the interlocking arrangement is wanting and they are simply apposed to one another (*Eriosoma*). At the enlarged proximal ends of both pairs of stylets are oval areas of glandular tissue known as the *retort-shaped organs*, whose function is problematical. In many Hemiptera the bases of the stylets are attached to the head-capsule by means of mandibular and maxillary levers. These latter are rods of chitin which extend outwards in a transverse direction, and afford attachment to certain of the stylet muscles. The stylets themselves are enclosed in a sheath (rostrum) formed almost entirely by the labium which is dorsally grooved for their reception. At its base, however, the labial groove is wanting and in this region the sheath is roofed over by the labrum. If the latter be raised with the point of a needle the stylets can be discerned beneath. Distally, the lips of the labial groove are approximated or fused to form a tube and, as the lumen of the latter is very small, the stylets fit tightly therein. In the majority of Hemiptera the labium is either 4-jointed (Pentatomidæ, Capsidæ, Lygæidæ, etc.) or 3-jointed (most Reduviidæ, Cicadidæ, Psyllidæ and Aleyrodidæ); in Coccidæ it is always short and 1- or 2-jointed. Its apex is provided with sensory

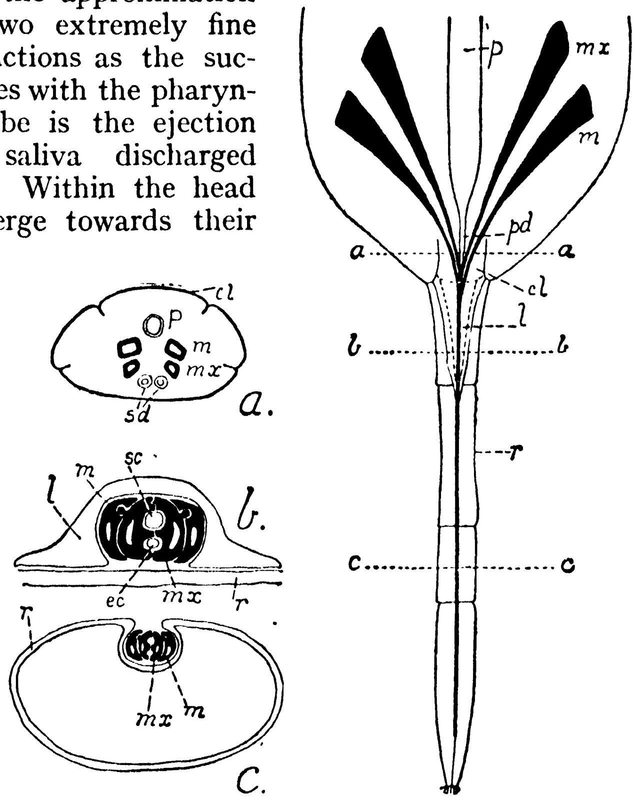

FIG. 347.—DIAGRAM OF THE MOUTH-PARTS AND ADJACENT REGION OF THE HEAD OF AN HEMIPTEROUS INSECT.

On the left are transverse sections across the regions bearing corresponding lettering; the magnifications of these sections are not uniform *cl*, clypeus; *ec*, ejection canal with salivary duct; *l*, labrum; *m*, mandible; *mx*, maxilla; *p*, pharynx; *pd*, pharyngeal duct; *r*, rostrum; *sd*, salivary ducts; *sc*, suction canal with pharyngeal duct.

setæ, and it performs no part in perforating the tissues of the plant-host Labial palpi are almost always wanting; in certain families, however. they are stated to be present, but there is no unanimity of opinion. Heymons (1896) finds that they are present in the embryo but atrophied in the adult, and that the so-called palpi are secondary organs. Leon, on the other hand, observes that they are present in *Nepa*, *Ranatra*, and certain Belostomatidæ. The hypopharynx is situated between the bases of the maxillæ, and is usually well chitinized though small and difficult to detect except in sections. It is pierced by the salivary duct and the latter passes forwards to open into the ejection canal; the dorsal wall of the hypopharynx forms a support to the floor of the pharyngeal duct (p. 355).

While at rest the rostrum is concealed by being flexed beneath the body, with its apex directed backwards. When the insect is about to feed, the rostrum is extended from its position of repose and inclined downwards. In the great majority of Hemiptera the stylets are only slightly longer than the rostrum, and consequently some mechanism is necessary by means of which the latter becomes retracted to admit of the insertion of the stylets into the plant. In Aphididæ, for example, this is brought about by the proximal portion of the rostrum being withdrawn or telescoped into the body (Davidson). In *Lygus*, and other Heteroptera, the stylets are able to penetrate the tissues owing, it is stated, to the bending or looping of the rostrum about its basal hinge (Awati). In Coccidæ the rostrum is very short, and the stylets extremely long, and the mechanism by which the latter are inserted into the plant, and afterwards withdrawn and looped within the body, is difficult to conceive.

The problem which requires solution is the method by which long, slender, pointed stylets can be forced to the requisite depth into the tissues of a plant. In those cases where the stylets are but little longer than the rostrum it has been usually explained that the action of the protractor muscles, applied at the bases of the stylets, force the latter into the plant, and that they are guided by the labrum and the grooved labium in their course. In *Psylla* Grove (1919) contends that this explanation is wholly inadequate owing to the great length of the stylets and their permanently looped condition. This author suggests that, by means of blood-pressure, the apex of the labium becomes distended and consequently grips the stylets tightly after the manner of a pair of forceps. The projecting portions of the stylets would be forced a short distance into the plant tissues. This being accomplished, the internal pressure would be slackened, which would result in the grip being released, and the rostrum would become slightly shorter, so that its apex would have travelled a short distance upwards along the stylets. The pressure being renewed, the grip is re-established and the stylets forced in a step further and so on, until the required amount of penetration may be accomplished.[1] It is evident that the range of action of the protractor muscles is much less than the depth to which the stylets often penetrate, and that their action alone is inadequate to explain the process. With regard to the mechanism of suction we have to consider the ejection of the saliva into the plant, and the flow of sap along the suction canal into the pharyngeal duct of the insect. There is no complete continuity between the walls of the salivary and pharyngeal ducts and those of ejection and suction canals respectively. The two ducts, however, project into their respective canals sufficiently far to allow for a regular flow of liquid,—in the one case outward and in the other inward. As a preliminary to piercing the plant tissue, the insect surveys the surface thereof by means of the apical setæ of the rostrum. The actual piercing apparently takes place by means of the mandibles, the maxillæ following closely afterwards. The saliva is forced down the ejection canal by means of the salivary pump, but the exact functions which it performs are difficult to ascertain. In several cases it is known to transform starch into sugar, but it certainly fulfils other uses. Thus, in some aphides the saliva also dissolves a passage for the stylets through the cell-walls and causes plasmolysis and dissolution of the cell-contents (Davidson). During the ascent of the sap in the minute suction canal capillarity, possibly aided by pressure exerted by the turgid plant-cells when pierced by the stylets, may be regarded as the preliminary process. This is followed by the active suction exerted by the divaricator muscles of the pharynx. The course of the stylets within the plant-tissues has been followed by Davidson in the case of *Aphis rumicis*. They pass intercellularly through the cortex, only occasionally perforating individual cells. On reaching the vascular bundles the cell-walls are punctured and the cell-contents sucked out. In this species the phloem is the chief source of the food supply, although other tissues, including the cortex and the mesophyll of the leaf, may be resorted to in the case of plants heavily infested by this aphid.

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[1] The whole subject of the mechanism of piercing and sucking in Hemiptera is admirably discussed by Weber (1928).

The **Thorax.**—The morphology of the hemipterous thorax has not been extensively investigated, but a comparison of a number of genera has been made by Taylor (1918) and a study of the sclerites of *Psylla* by Weber (1928). Among Heteroptera the pronotum is tolerably uniform in its characters : it is always large, rarely marked off into separate sclerites, and forms the greater part of the thorax when viewed from above. The mesonotum frequently exhibits a five-fold division, thus presenting the maximum number of sclerites. Of these the most prominent is the scutellum, which is always well developed : in certain Pentatomidæ it extends posteriorly to the extent of entirely covering the wings, and imparts to the insect an apterous appearance. The metanotum is very variable : it may be well developed, as in *Anasa*, or reduced to a small region concealed beneath the mesoscutellum. It is never conspicuous, and is covered by the unexpanded wings. The sternites are, for the most part, fused with the respective pleura.

Among Homoptera there is more diversity of structure, and *Cicada* may be regarded as fairly typical of the sub-order. The pronotum is almost always small and frequently collar-like, except in Membracidæ where it assumes incredibly bizarre and grotesque forms and extends backwards over the abdomen. The mesothorax is the largest and most typical region, exhibiting the primary divisions into prescutum, scutum, scutellum and postscutellum. In the Fulgoroidea it bears well-developed tegulæ, which are vestigial or absent in these species with reduced wings. The metanotum is usually well developed, and in Jassidæ it is nearly as long as the mesonotum.

The **Wings.**—Among Heteroptera there is a marked difference in the consistency of the two pairs of *wings*, as is implied by the name of that sub-order. The fore-wings are termed hemelytra (*hemi-elytra*) and their proximal area is horny, resembling an elytron, only the smaller distal portion remaining membranous (Fig. 349). The hind-wings are always membranous and, in repose, are folded beneath the hemelytra.

The hemelytra (Fig. 348) exhibit much diversity of structure and, for this reason, have been largely utilized for purposes of classification. The hardened basal portion is composed of two regions—the *clavus* or narrower area next to the scutellum (when the wings are closed), and the *corium* or remaining broader portion. In the families Ceratocombidæ and Anthocoridæ a narrow strip of the corium, bordering on the costa, is demarcated from the remainder, and is known as the *embolium*. In the Capsidæ a triangular apical portion of the corium is separately differentiated to form the *cuneus*. Among Tingidæ the differentiation into corneus and membranous regions is less distinct. In some cases the membranous area is much reduced or wholly absorbed, but in the Henicocephalidæ the hemelytra are entirely membranous. The two pairs of wings exhibit evident departures from the primitive venational type and the most generalized tracheation has been found in Pentatomidæ (vide Comstock).

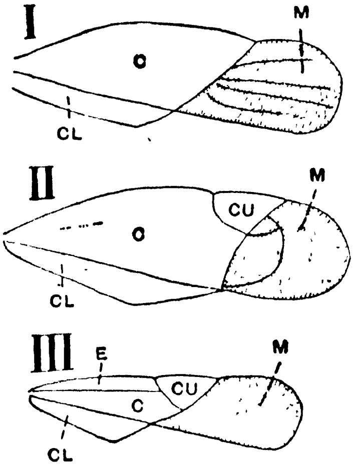

Fig. 348.—Diagrams of the Hemelytra of—I, A Lygæid; II, A Capsid; III, An Anthocorid.

C, corium; *CL*, clavus; *CU*, cuneus; *E*, embolium; *M*, membrane.

Among Homoptera the fore-wings are of uniform texture (Fig. 350) and are frequently of harder consistency than the hind pair. Apterous forms are the rule in female Coccidæ and Aphididæ (sexuales), as well as occurring in the agamic generations of the latter family; both apterous and alate males are sometimes present in both Aphididæ and Coccidæ. Although there is great diversity of venation which is dealt with under the different families, the pre-existent tracheæ have been extensively studied in the nymph, and it is thus possible to determine the homologies of the wing-veins.

The little-understood phenomenon of alary polymorphism is prevalent in different families. That is to say, in the same species there may be two or more forms of alary organs which, furthermore, may be correlated with sex or may not. There are two well-marked types of individuals,— the apterous and macropterous, sometimes with intermediates or brachypterous forms. The phenomenon is evident, for example, in the Hydrometridæ, Anthocoridæ and Reduviidæ among Heteroptera, and certain Fulgoroidea (Delphacidæ) and Jassidæ among Homoptera. It is particularly well seen in the British species of *Liburnia*. In *Perkinsiella* there is much specific variation in this respect: thus *P.*

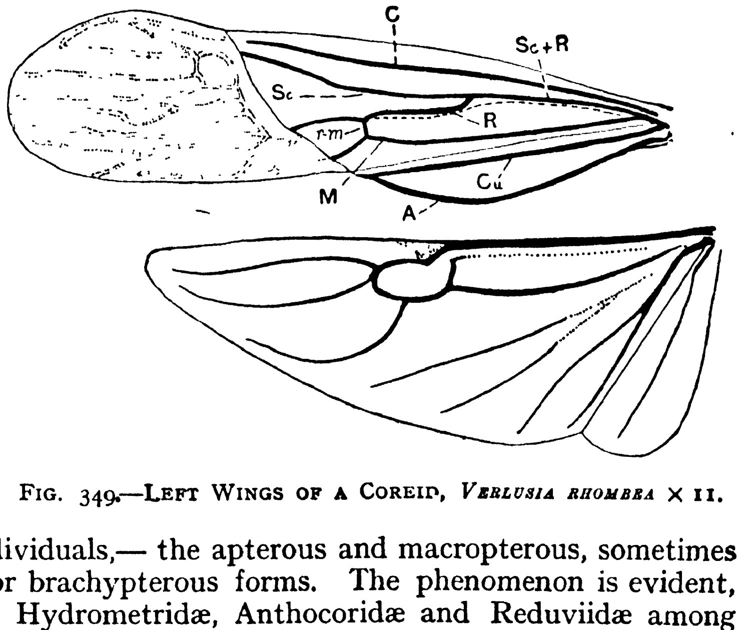

Fig. 349.—Left Wings of a Coreid, *Verlusia rhombea* × 11.

sacchariсida has macropterous males and polymorphic females, while in *P. vitiensis* and *vastatrix* both sexes are dimorphic.

In certain African Reduviidæ (*Edocla* Stål) the males are winged and the females apterous and physogastric: in other species of the genus both sexes are alike and physogastric. In *Paredocla* Jeann. there are both winged and apterous males; the latter resemble the females, which are also apterous, and all forms are found together (Jeannel, *Voy. Afriq. Orient.*, Hemiptera, 3, 1919).

Many explanations have been advanced to account for alary polymorphism (vide Kirkaldy, 1906). It has been variously correlated with climate, season, mimicry, capability for leaping or rapid locomotion, and mode of life, whether arboreal or otherwise. Thus, in Africa, Jeannel states that most of the apterous and brachypterous genera of Reduviidæ inhabit the hotter regions. In the European *Pyrrhocoris apterus* both pairs of wings may be either normally developed, or reduced to merely the horny basal portions of the hemelytra, and the two forms vary very greatly both in local and seasonal occurrence. The phenomenon offers a wide field for research, particularly from the genetic point of view.

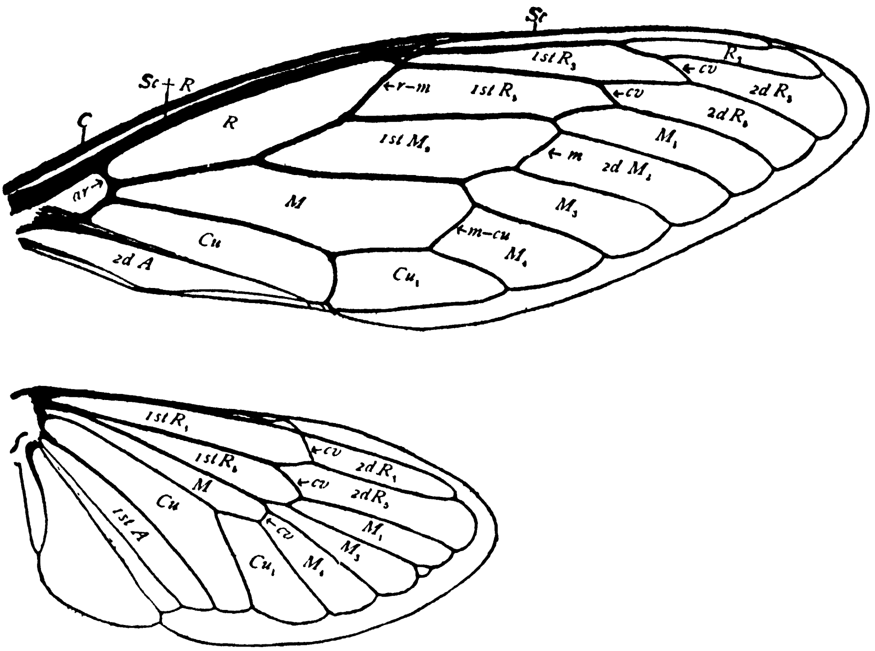

FIG. 350.—RIGHT WINGS OF A CICADA.

From Comstock, *after* Comstock and Needham. (N.B.—Vein 1A of Comstock = Cu_2 of Tillyard.)

The **Abdomen.**—In its least modified condition the abdomen often consists of eleven recognizable segments as in *Cicada* (Berlese) and several other genera of Homoptera (Heymons). As a general rule, however, suppression and reduction have taken place to a greater or less degree. Thus in *Anasa* Tower (1913) finds there are 9 segments in the male and 10 in the female. In *Notonecta* the 1st segment is greatly reduced, but segments 2–11 are evident: in *Nepa* and *Ranatra* the 1st tergum and the 1st and 2nd sterna are atrophied, but the remaining segments to the 11th are recognized by Berlese. In Psyllidæ Crawford also finds evidence of 11 original segments; of these the 1st, 2nd and 3rd are either suppressed or much reduced.

Among Aphididæ the number is difficult to determine and most observers conclude there are nine visible segments.

Among Heteroptera a well-developed ovipositor is present in a few families, notably in the Nepidæ and Notonectidæ, where it consists of three pairs of gonapophyses. A valvular ovipositor is present in the Auchenorhyncha but, for the most part, is reduced or wanting among the Sternorhyncha.

Sound-producing Organs are of frequent occurrence among Heteroptera and may be grouped under five chief types.

(1) The PROSTERNAL FURROW of many Reduviidæ and Phymatidæ studied by Handlirsch (1900). This furrow is cross-striated and stridulation is produced by the rugose apex of the rostrum working thereon; it is well seen in *Reduvius personatus* and *Coranus subapterus*.

(2) The STRIGOSE VENTRAL AREAS of certain Pentatomidæ (Scutellerinæ). According to Handlirsch these are found on either side of the median line of the 4th and 5th abdominal segments. On the inner side of the hind tibiæ are wart-like tubercles, each bearing a subapical tooth. When the insect bends the tibia against the femur, and again extends it, the spinous tubercles pass across the strigose areas, thus enabling the insect by rapidly repeating the movements to produce an audible sound.

(3) The PEDAL STRIDULATING ORGANS of Corixidæ. The anterior tarsus bears a row of teeth and the anterior femur is provided with a stridulatory area consisting of rows of minute pegs. It appears that the tarsal "comb" of the left leg is drawn obliquely across the femur of the right leg and *vice versa*, and in this manner sound is produced (Kirkaldy, 1901); in the females the mechanism is much less highly developed. According to Handlirsch sound is produced by drawing the tarsal comb across the ridged clypeus.

(4) COXAL STRIDULATORY ORGANS. In *Ranatra* Bueno (*Can. Ent.* 1905) describes two opposing rasps, one on each coxa near the base with longitudinal striations, the other on the inner surface of the cephalic margin of the lateral plate of the coxal cavity. The latter plate is exceptionally thin and probably functions as a resonating organ.

(5) The DORSAL STRIDULATORY ORGANS which are found in both sexes of *Tessaratoma papillosa*. The sound-producing organ consists of a striated surface or file situated one on either side of the dorsum of the abdomen close to the metathorax. On the under-surface of each wing, near the base, is a comb of strong teeth. The sclerite supporting the files is able to move backwards and forwards across the comb (Muir, 1907). Dorsal stridulating organs are also described in the Corixidæ in addition to those mentioned under (3).

Among Homoptera, the sound-producing organs of the Cicadidæ are complex structures peculiar to the family, and situated one on either side of the ventral aspect of the base of the abdomen (vide p.102). The remaining Auchenorhyncha are usually regarded as being silent, but Kirkaldy (1907) states that several leaf-hoppers possess the power of stridulation.

Spiracles.—According to Schiödte 10 pairs of spiracles are normally present in Heteroptera, and this conclusion is confirmed by Handlirsch. They are present on the following segments; 1st pair, on the membrane between the pro- and meso-thorax, and only to be observed with difficulty: 2nd pair, between the meso- and meta-thorax: 3rd pair, dorsal lying between the metanotum and 1st abdominal tergum, hidden by the wings:

4th and following pairs, on the ventral side of the pleural folds of the consecutive abdominal segments. This general rule is subject to modification particularly in aquatic families. Thus in *Nepa* there are 10 pairs of open spiracles in the nymph, but in the adult most of these are either closed or non-functional. Maulik (1916) regards the first three pairs as being functional although closed ; the only other functional pair is at the base of the respiratory siphon. The 4th, 5th and 9th pairs have atrophied and the 6th, 7th and 8th are highly modified sieve-like structures which are regarded by Doges, and also Baunacke (1912), as being modified into sensory organs. The spiracles of *Notonecta* have been investigated by Brocher (1909), who states that there are 9 pairs.

In the Auchenorhyncha there are 10 pairs of spiracles as a general rule, but among the Sternorhyncha there is a wide range of variation. In Aphididæ there are usually 9 pairs, situated respectively on the pro- and meta-thorax and on the first 7 abdominal segments. Among Psyllidæ Witlaczil (1885) finds 2 thoracic and 7 abdominal spiracles in the nymph of *Trioza,* while in the adult *Psylla mali* Awati (1915) states there are 2 thoracic and 3 abdominal pairs. In the Aleyrodidæ the nymphs are closely applied to the leaf surface, and as the spiracles lie ventrally they are concealed. Air is conveyed thereto by means of special breathing folds of the integument. Two pairs of thoracic spiracles are present, —one pair between the anterior legs and the other pair between the posterior legs. Spiracles are also present behind the 2nd thoracic pair apparently on the 1st abdominal segment, and a 4th pair exists alongside the vasiform orifice. Vestigial spiracles are apparently found in some genera on other of the abdominal segments. In the adult the distribution of the spiracles is very much the same as in the nymph. The respiratory system of both Psyllidæ and Aleyrodidæ, however, requires detailed investigation.

In the nymphs and females of the Coccidæ there are commonly two pairs of spiracles on the ventral aspect of the thorax ; abdominal spiracles are present, however, in certain groups (Ferris, *Can. Ent.* 1918). The primitive number of 2 thoracic and 8 abdominal pairs is found in *Xylococcus* (Oguma, 1919) ; in *Orthezia* (List, 1887) and *Monophlebus* (Savage) there is one pair less on the abdomen. In *Icerya purchasi* the abdominal spiracles are reduced to 2 pairs, and in certain other species of that genus there are at least 3 pairs present (Ferris).

Internal Anatomy

The **Alimentary Canal.**—A true mouth is absent, and the actual entrance into the digestive system is the aperture of the suction canal, which is situated at the apex of the maxillary stylets. Towards the base of the latter the suction canal communicates with the *pharyngeal duct,* which is the narrow continuation of the pharynx into the labral region. The *pharynx* proper is the principal organ of suction, and its dorsal wall is provided with powerful divaricator muscles. In the region of the epipharynx there is, in most Hemiptera, a *gustatory organ* whose sensory cells communicate with the lumen of the pharyngeal duct through perforations in a chitinous plate, which is a specialized development of the epipharyngeal membrane. The greater part of the digestive canal is highly modified in both sub-orders though in totally different directions. In Heteroptera the *mid-gut* is frequently divisible into four sharply differentiated tracts (Fig. 351): (1) An anterior sac-like chamber; (2) a tubular region; (3) an ovoid chamber smaller than the first; (4) a narrow tubular portion from which, in many families, numerous gastric cœca take their origin. In certain of the strictly predaceous groups these divisions are less evident, and the tubular 4th region is absent in those families which lack the gastric cœca. The hind intestine is very contracted and consists of a small bladder-like chamber, which receives the Malpighian tubes, and a very large rectal chamber, often much more extensive than the 1st division of the mid-gut. The remarkable *gastric cœca* have been studied by Glasgow (1914), and they present many variations in form, number and arrangement. In *Blissus leucopterus* there are 10 finger-like cœca present, in *Anasa tristis* there are several hundreds in the form of closely compacted pockets, while in *Dysdercus* they are few in number (6 in the male and none in the female). The cœca are invariably filled with bacteria and, furthermore, the association is hereditary, the organisms being present in the gut of the developing embryo. Their function appears to be that of inhibiting the growth of foreign bacteria, and so excluding the latter from the mid-gut.

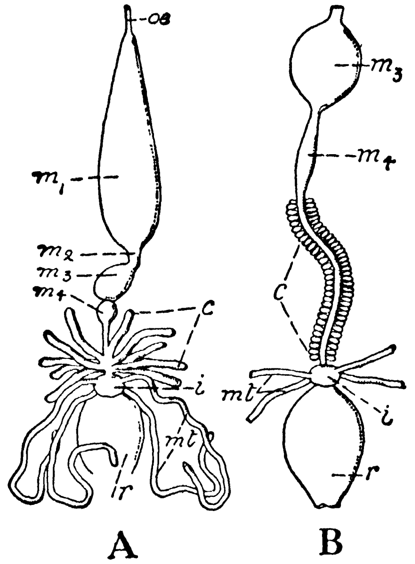

Fig. 351.—Digestive System of Lygæidæ. A, *Blissus leucopterus*. B, *Œdancala dorsalis* (Posterior Portion only).

c, gastric cœca; *i*, ileum; m_1–m_4, chambers of mid-intestine; *mt*, Malpighian tubes; *œ*, œsophagus; *r*, rectum. *After* Glasgow (reduced).

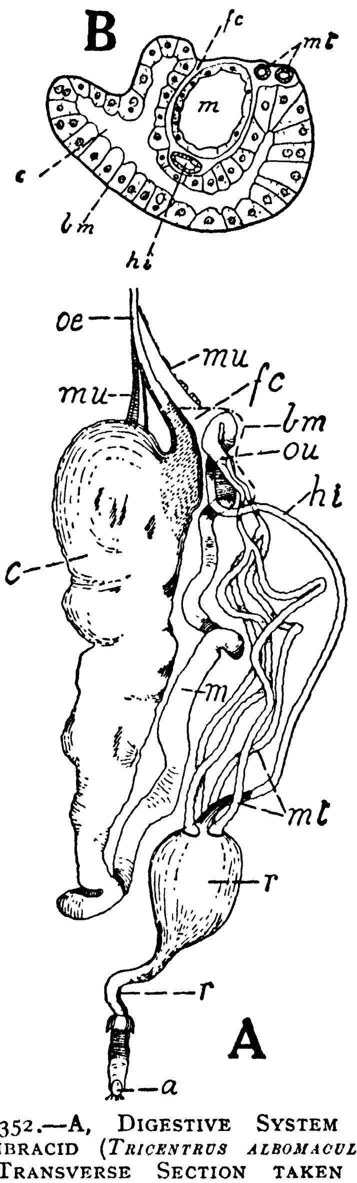

Fig. 352.—A, Digestive System of a Membracid (*Tricentrus albomaculatus*). B, Transverse Section taken just below Line ou in A.

a, anus; *bm*, basement membrane; *c*, crop; *fc*, filter chamber; *hi*, hind-intestine; *m*, mid-intestine; *mt*, Malpighian tubes; *mu*, muscles; *oe*, œsophagus; *ou*, point of origin of Malpighian tubes; *r*, rectum. *After* Kershaw.

Among many Homoptera the œsophagus leads into a very capacious crop which occupies a large part of the abdominal cavity. The mid-gut is long and tubular and reflected on the crop in an ascending manner, with the result that its junction with the hind intestine comes to lie very far forwards alongside the œsophagus (Fig. 352). Owing to this disposition, the insertions of the Malpighian tubes are likewise anteriorly situated, and these organs, together with the mid-gut and the hind-intestine, form a complex coil of tubes lying in the thorax (Kershaw, *Psyche*, 21). In the Membracid *Tricentrus albomaculatus* Kershaw (*Ann. Soc. Ent. Belg.* 57) states that the basement membrane, and the external muscles of the crop and of the base of the œsophagus, separate from the epithelial walls of those parts, and enclose the twisted knot formed by the above visceral complex. The result is that the latter comes to lie in a chamber bounded externally by the basement membrane. A similar arrangement of the viscera is found in Cercopidæ (Licent, *Bull. Soc. Ent. Fr.* 1911), in Coccidæ and other Homoptera. The chamber or cavity thus formed is termed by Berlese the *filter chamber*. This authority suggests that, owing to the large surface presented by the mid-gut, where it is applied to the wall of the œsophagus and crop, the excess of liquid in the food will pass directly by osmosis through the intervening walls to the mid-gut, and thence through the wall of the latter into the hind intestine. In this manner liquid is quickly eliminated, while solid matter passes by the usual course through the whole digestive system.

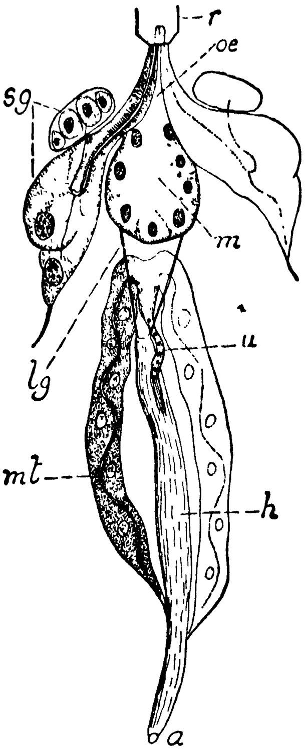

FIG. 353.—DIGESTIVE SYSTEM OF *LEPIDOSAPHES FULVA* × 80

lg, ligament; *oe*, œsophagus; *r*, rostrum; *sg*, salivary glands; *u*, ureter. Other lettering as in Fig. 338. *After* Berlese, *Riv. di Pat. Veg.* 5.

In the Diaspine Coccids the mid-gut is a closed sac (Fig. 353), entirely disconnected from the hind intestine, and the digestive juices render the food-contents capable of passing by osmosis into the main hæmocœlic cavity. The waste substances therefrom are then taken up by the greatly enlarged Malpighian tubes (Berlese). Childs (1914), although not disputing Berlese's views as to digestion in these insects, states that continuity with the hind-intestine obtains by means of an extremely short solid cord, and that the usual condition observed by Berlese is due to its rupture by the action of fixing fluids prior to section cutting.

The prevalent number of *Malpighian tubes* in Heteroptera is 4, but in *Lethocerus* there are 2 (Locy). Among Homoptera they are more variable; thus, in Membracidæ there are 4 united proximally in pairs (Kershaw), and the same number is present in *Cicada*. Among Coccidæ there are generally 2 tubes of very large calibre and but little convoluted, but in *Icerya* there are 3 (Johnston) and in *Xylococcus* 4 (Oguma). Among Aphididæ Malpighian tubes are absent.

Salivary Glands.—These organs exhibit a marked uniformity of structure among Heteroptera, and have been very fully investigated by Bugnion and Popoff (1908, 1910) and Faure-Fremiet (1910). The principal gland (Fig. 354) is ordinarily bi- or pluri-lobed and situated in the thorax; the accessory gland is most often filiform. The main salivary duct arises at the point of junction of the lobes of the principal gland and, in the same region, it receives the long sinuous duct of the accessory gland of its side. The two main ducts of opposite sides converge to form a common canal opening into the *salivary pump*. In the zoophagous forms (*Harpactor*, *Reduvius personatus* and the Cryptocerata) the accessory gland is thin-walled and modified to form a reservoir. In some forms (*Naucoris*) the principal gland is very large and may extend into the abdomen.

In *Fulgora* there are three pairs of glands corresponding to the anterior and posterior lobes of the principal gland and the accessory gland of Heteroptera. In *Cicada* there are likewise three pairs of glands. Among aphides 2 pairs of simple sac-like glands are located in the prothorax in *Eriosoma* and *Lachnus*; in *Phylloxera vastatrix* and *Chermes lapponicus* 3 pairs have been described. Among Coccids the glands are bilobed in *Lepidosaphes* and *Xylococcus*; in *Icerya* each gland is reduced to 3 multinucleate spherical cells (Johnston).

The *salivary pump* or "syringe" is a very characteristic structure in Hemiptera and is attached anteriorly to the hypopharynx. It is provided with stout muscles and functions as a force-pump, propelling the saliva down the ejection canal.

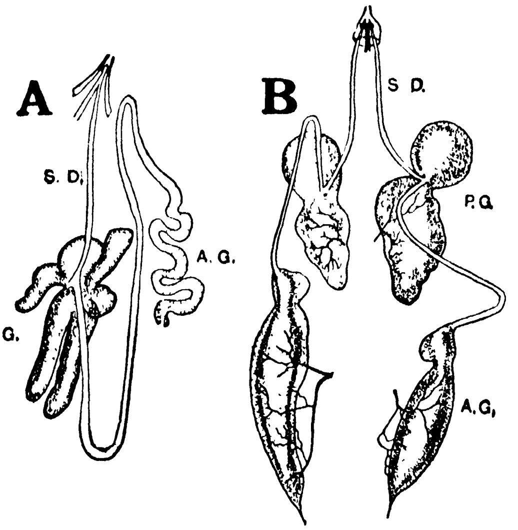

Fig. 354.—Salivary Glands of A, *Lygæus apuans*: B, *Notonecta maculata*.

SD, salivary duct; *AG*, accessory gland; *PG*, principal gland. *After* Bugnion, 1908 (reduced).

Odoriferous Glands.—Odoriferous or repugnatorial glands are characteristic of a large number of Heteroptera, and open to the exterior by means of a pair of ventral pores or slits situated near the coxæ of the hind-legs. Each opening is surrounded by an evaporating surface, which retains the secretion while it volatilizes and prevents its more extended diffusion: the surface of this area is usually finely rugose or granulated (Schiödte).

In *Lethocerus* the glands form a pair of convoluted tubes and their odour is said to resemble that of ripe pears or bananas (Locy, 1884): very similar glands have been found by Bordas in *Gerris*. In the nymphs the meta-thoracic glands are wanting, their place being taken by dorsal abdominal glands which assume the form of small integumentary invaginations.

Wax Glands.—These are prevalent in many Homoptera. They are usually unicellular and may occur either singly or in groups (vide p. 147). They are well exhibited in the oriental *Phromnia marginella*, where they are situated beneath series of chitinous plates on the dorsum of the abdomen: each plate is studded with pores which are the apertures of the wax glands. In various Aphididæ (*Pemphigus*, *Adelges*, *Eriosoma*, *Lachnus*, etc.) the plates are segmentally arranged in longitudinal series. The product of the glands is commonly in the form of a powdery secretion, or of dense flocculent threads.

The **Nervous System** exhibits a very uniform and complete degree of concentration. The abdominal ganglia are to a large extent fused up with the thoracic, though the connectives persist as the main single or paired abdominal nerve which gives off lateral segmental branches. The most extensive studies are those of Brandt (1878) and the following grades of concentration in the ventral ganglia are recognizable.

(1) Three ventral ganglia present (*Lygæus*, *Capsus*, *Notonecta*, *Aphrophora*, etc.). The infra-œsophageal and 1st thoracic ganglia are separate, while the abdominal ganglia are fused with those of the 2nd and 3rd thoracic segments to form a common centre.

(2) Two ventral ganglia present (Aphididæ). The first is the infra-œsophageal ganglion, while the thoracic and abdominal ganglia are merged into a common centre. In the Nepidæ the prothoracic and infra-œsophageal ganglia are apparently fused since the nerves supplying the first pair of legs issue from the latter centre.

(3) A single ganglionic centre formed by the coalescence of all the ventral ganglia (*Hydrometra* and Coccidæ).

The **Dorsal Vessel** has been very little investigated: a 5-chambered heart is present in *Lethocerus* (Locy), but there is no definite dorsal vessel in Coccidæ. Among Aphididæ it was first described by Witlaczil (1882), and Mordwilko (1895) refers to a chambered vessel in *Trama*. No trace, however, has been found in *Phylloxera* (Dreyfus) or in the apterous viviparous female of *Eriosoma* (Davidson).

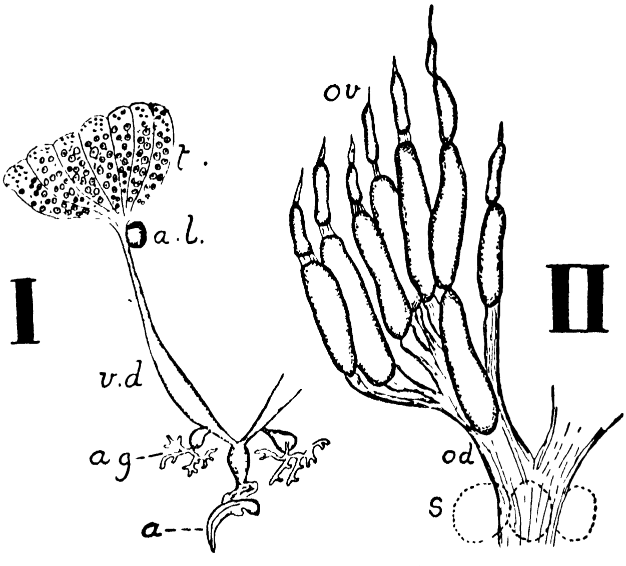

FIG. 355.—REPRODUCTIVE ORGANS (RIGHT SIDE ONLY) OF *CIMEX ROTUNDATUS*. I Male; II Female.

a, ædeagus; *a g*, accessory gland; *a l*, accessory lobe of testis; *od*, oviduct; *ov*, ovary; *s*, spermathecæ; *t*, testis; *vd*, vas deferens. Adapted from Patton and Cragg.

Pulsatile Organs occur in various aquatic genera. They are present in each pair of legs and, owing to the opacity of the integument, are best observed in the nymphs. Brocher (1909A) has studied these organs among Cryptocerata: they are present at the base of the 1st tarsal joint of the anterior legs, and at the base of tibia in the other pairs. In *Ranatra* each organ consists of a pulsatile membrane lying longitudinally in the cavity of the limb; it serves to ensure the circulation of the blood in the extremities. Pulsatile organs are also present in the tibiæ of *Philænus* (Gahan) and in aphides (Richardson).

Reproductive System (Figs. 355, 356).—Each ovary has a variable number of ovarioles which are composed of a small number of follicles (usually 1 to 4). In structure the ovarioles are commonly of the acrotrophic type, but their histology has not been extensively studied in this order: in certain Heteroptera protoplasmic cords connect the nutritive cells with the developing oocytes. In this sub-order the ovarioles are few in number, generally 4 to 7 (*Lethocerus* and *Ranatra* 5, *Triatoma* and *Cimex* 7). Holmgren (*Zool. Jahrb. Syst.* 12) figures the reproductive system of certain Auchenorhyncha and the ovarioles varied in the examples studied from 3 in *Eupteryx* to 9 in *Philænus*. Among Sternorhyncha there are 8 or 9 very short ovarioles in *Psylla mali* (Awati), but in *P. alni* there are 40–50 (Witlaczil). In Coccidæ they are numerous, each consisting of a single follicle arising from a wide oviduct; in *Icerya* (Johnston, 1912) the oviducts are united anteriorly, forming a broad loop. In Aphididæ the number of ovarioles varies in individuals of the same species, and different phases of the life-cycle. Thus, in *Phylloxera vastatrix*, in the apterous parthenogenetic forms they vary from one or two to thirty according to conditions (Foa), each containing two follicles; in the alate females there are usually two, and in the sexuales of this species and also *Eriosoma lanigera* (Baker, 1915) there is a single unpaired unilocular ovariole. Spermathecæ are very generally present among Hemiptera: in *Triatoma* they are small and paired, but there is usually a single dorsal or ventral organ, often of complex structure. Accessory glands, two or three in number and either tubular or globose, are of general occurrence, but are wanting in the Diaspine Coccidæ (Berlese).

In *Cimex* there is a small rounded body, known as the organ of Berlese, which is situated in the ventral region of the abdomen (vide Cragg, *Ind. Journ. Med. Res.* 8, 1920). It is usually unpaired and lies on the right side, its external opening being in close association with a small longitudinal incision on the 4th sternum. The organ functions as a copulatory pouch which receives the spermatozoa discharged during coition. After the latter process is accomplished the spermatozoa pass in large masses through the hæmocœl into the spermathecæ. The latter organs are stated to be unconnected with the common oviduct and it appears that the spermatozoa migrate from the spermathecæ through the walls of the paired oviduct in order to reach the eggs. It is probable that the excess spermatozoa are utilized by the female as nutriment during oviposition—a process which is termed by Berlese "hypergamesis"; when and by what means absorption occurs needs investigation.

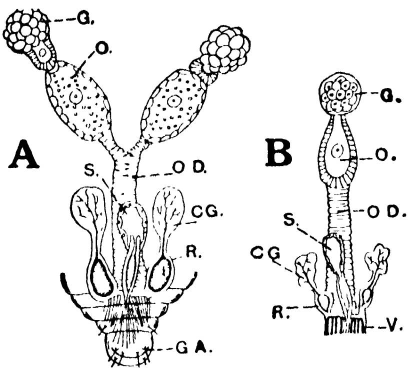

FIG. 356.—FEMALE REPRODUCTIVE ORGANS OF *PHYLLOXERA VASTATRIX*.

A, of winged agamic form: B, of sexual form *CG*, colleterial gland and reservoir *R*, ; *G*, germarium; *GA*, genital aperture; *O*, ovum; *OD*, common oviduct; *S*, spermatheca; *V*, vagina. *After* Balbiani.

The male organs are so variable in form that a brief general description is very inadequate. It may be mentioned, however, that in *Ranatra fusca* each testis consists of six follicles enclosed in a scrotum, and the vas deferens on either side is enlarged to form a vesicula seminalis (Marshall and Severin, 1904). In *Cicada orni* the testes are ovoid with long, slender vasa deferentia; paired filiform accessory glands are present, together with an unpaired vesicula seminalis, situated at the point of union of the vasa deferentia (Dufour). In Coccidæ the male organs are very simple: the testes are in the form of ovoid sacs, either with or without a vesicula seminalis.

The **Pseudovitellus.**—In most Homoptera there is, in the abdomen, a mass of cell-tissue,—the pseudovitellus or *mycetome*. In Aphididæ the appearance and distribution of this tissue depends upon the stage in development of the individual. It takes the form of small groups of large rounded conspicuous cells and is regarded by Witlaczil as being excretory in function; other authors ascribe to it a nutritive value. According to Sulc (*Sitz. König. Bohm. Ges. Wiss., Prag,* 1910) and also Buchner (*Arch. Protistenk.* 1912) the organ contains great numbers of symbiotic microörganisms which are harboured in cells known as mycetocytes

The association is claimed to result in the microörganisms profiting by the protection and nutrient matter which they receive, while they benefit the host as absorbers of waste products or excess food materials. Buchner has also shown that a certain number of the organisms migrate to the eggs and are thus transmitted from one generation to another. For other studies on the subject see Buchner (1930) and Uichanco (1924).

Metamorphoses

The eggs of Heteroptera (Fig. 357) exhibit great diversity of form, chorionic structure, and colouring (vide Heidemann, 1911). The various types are peculiarly constant for different families and, when further studied, will evidently afford characters of classificatory value. Many are adorned with delicate sculpturing and spines or filiform appendages. In several families (Pentatomidæ, Coreidæ, Reduviidæ, Phymatidæ, Cimicidæ, etc.) there is a conspicuous operculum (Fig. 363), often of complex structure, which is usually liberated at the time of hatching. At the upper pole of the egg, notably among Pentatomidæ, Tingidæ, and Reduviidæ, there is a circlet of peculiarly shaped chorionic processes disposed around the rim of the operculum. These were originally termed by Leuckart "seminal cups" from the belief that they afforded a means by which the spermatozoa entered the egg: by certain more recent observers they are regarded as a mechanism to ensure the access of air to the interior of the egg. Whether their function is micropylar or otherwise is unsettled in the absence of direct observation. A T-shaped denticle, or egg-burster, is present in the newly hatched nymphs of Pentatomidæ and Coreidæ; it is cast during the first moult, before the insect completely issues from the egg, and is usually found adhering to the empty chorion.

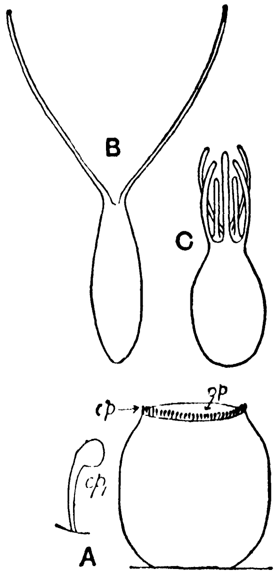

FIG. 357—EGGS OF HETEROPTERA.

A, a Pentatomid, *Euschistus* (*after* Heidemann). B, *Ranatra* and C, *Nepa* (*after* Schouteden). *op*, operculum; *cp*, chorionic processes; cp_1, one of the latter more enlarged.

Among the Homoptera the eggs, as a general rule, are ovoid and of much simpler structure: in the Aleyrodidæ and *Psylla*, however, they are often provided with a filamentous prolongation at one pole (p. 379): an egg-burster is present in aphides.

Postembryonic development in Hemiptera is gradual, but colour changes are often very marked. The most sharply pronounced modifications are concentrated in the last ecdysis from the final nymph to the imago. The external morphological changes during development involve the joints of the antennæ and tarsi, the latter frequently not attaining their full number until the adult instar. The shape of the head and thoracic segments, more particularly the pronotum, undergo marked changes in different instars. Wing rudiments are small or scarcely distinguishable in the 3rd instar but are evident in the 4th. Among Heteroptera the usual number of instars (including the adult) is six; *Dindymus sanguineus*, however, is exceptional in passing through nine instars (Muir and Kershaw).

In Homoptera the number of instars is subject to great variation; in *Psylla* and *Empoasca* there are six, in aphides five except in the apterous

Phylloxerinæ, where there are four, and the latter number is recorded in *Aleyrodes*. The highest observed number is seven (in *Cicada septendecim*) and the lowest in Coccidæ where, as a rule, there are three instars in the females, and four in the males. In the males of Coccidæ the last instar but one is the pupa, and the same obtains in both sexes of Aleyrodidæ.

Classification

The growth of detailed knowledge during the last 25 years has resulted in the recognition of an increasing number of families of Hemiptera, and scarcely any two authorities are in complete agreement with regard to the system of classification employed (vide Horvath, 1911). The only general catalogue of the Hemiptera of the world is that of Lethierry and Severin (1893-96) which, however, is incomplete and only comprises the Heteroptera (excluding Capsidæ and Cryptocerata), but has been brought up to date by Bergroth (1913). An admirable classified and annotated guide to much of the more important taxonomic and faunistic literature is provided by Oshanin (1916), and is indispensable to all who require a detailed acquaintance with the order. The same author's catalogue of the palæarctic species (1906-10) and his later list (1912) are also valuable. Van Duzee (1917) has catalogued the N. America forms giving very full synonomy.

Sub-order 1. HETEROPTERA

Wings generally overlapping on the abdomen, the fore pair usually membranous apically. Base of rostrum usually not touching anterior coxæ Gular region chitinized. Pronotum large; tarsi usually 3-jointed. Metamorphosis incomplete.

Series I. GYMNOCERATA

Antennæ conspicuous, freely movable in front of the head.

Series II. CRYPTOCERATA

Antennæ concealed either on underside of head or in fovæ beneath the head. Aquatic.

Sub-order 2. HOMOPTERA

A very diverse assemblage. Wings usually sloping over sides of body, the fore pair of uniform consistency throughout: apterous forms frequent. Base of rostrum extending between anterior coxæ. Gular region membranous or wanting. Pronotum small; tarsi 1- to 3-jointed. Metamorphosis usually incomplete, sometimes complete in male, more rarely so in female.

Series I. AUCHENORHYNCHA

Antennæ very short with a terminal arista; rostrum plainly arising from the head. Tarsi 3-jointed. Active forms, capable of free locomotion.

Series II. STERNORHYNCHA

Antennæ well developed without conspicuous terminal arista, sometimes atrophied. Rostrum apparently arising between anterior coxæ, or wanting. Tarsi 1 or 2-jointed. Species often inactive, or incapable of locomotion (in the female).

Sub-order I. HETEROPTERA

The classification of this sub-order has been discussed by Reuter (1910) who revised the various systems proposed and criticized the values of the characters utilized. In addition to this work the reader should also consult Schiödte (1870), who lays great stress on the method of articulation of the hind coxæ, and the tentative paper by Kirkaldy (1908). In view of the want of agreement in the classifications proposed by recent authorities (Horvath for example recognizing no less than 46 families) we have followed the more antiquated scheme adopted by Distant (1902, Vol. I), which will be found applicable to the needs of the non-specialist. The time-honoured division of the Heteroptera into Gymnocerata and Cryptocerata separates these two groups on obvious antennal characters and divides the truly aquatic forms from those which are either only surface dwellers or terrestrial in habit. It involves, however, the inclusion of the Nepidæ in the Cryptocerata, whereas recent research indicates that their affinities lie near the Reduviidæ.

The standard work on the British Heteroptera is that of Saunders (1892) and their biology is very fully treated by Butler (1923). For the European species the most important treatises are those of Fieber (1861) and Stål (1870-76); the latter author's monograph of the African forms is also valuable. Puton's synopsis of French Heteroptera (1878-81) is very practical and most of the European species may be identified with its aid.

The following key will aid in the identification of the families of **Gymnocerata.**

1 (30).—Abdomen devoid of ventral silvery pubescence: non-aquatic.
2 (3).—Parasitic: ovoid, flattened insects; hemelytra vestigial; no ocelli; rostrum and tarsi 3-jointed. Cimicidæ (p. 368)
3 (2).—Not as in (2).
4 (5).—Scutellum very large, at least reaching base of membrane or middle of abdomen. Pentatomidæ (p. 364)
5 (4).—Scutellum not reaching the base of membrane or middle of abdomen.
6 (25).—Cuneus absent: meso- and meta-pleura simple.
7 (20).—Tarsi 3-jointed.
8 (15).—Rostrum straight, lying against under surface of head.
9 (12).—Antennæ inserted on upper part of sides of head.
10 (11).—Legs moderately long, apices of femora not clavate. Coreidæ (p. 365)
11 (10).—Legs long and slender, femora clavate at apices. Berytidæ (p. 365)
12 (9).—Antennæ inserted below a line drawn from the eye to the apex of face.
13 (14).—Ocelli present. Lygæidæ (p. 365)
14 (13).—Ocelli absent. Pyrrochoridæ (p. 366)
15 (8).—Rostrum bent at base and not lying in contact with under surface of head.
16 (17).—Rostrum long: ocelli between the eyes. Saldidæ (p. 369)
17 (16).—Rostrum short: ocelli, when present, behind the eyes.
18 (19).—Hemelytra complete. Reduviidæ (p. 367)

19 (18).—Hemelytra entirely membranous.	Henicocephalidæ (p. 367)
20 (7).—Tarsi of less than 3 joints.	
21 (24).—Anterior legs normal.	
22 (23).—Hemelytra with cellular or reticulate pattern.	Tingidæ (p. 366)
23 (22).—Hemelytra without such pattern.	Aradidæ (p. 366)
24 (21).—Anterior legs short and stout, femora thick, tibiæ curved and pointed: tarsi often absent.	Phymatidæ (p. 367)
25 (6).—Cuneus present: meso- and meta-pleura subdivided.	
26 (29).—Embolium present.	
27 (28).—Antennæ elongate and slender with long hairs: 3rd and 4th joints together twice as long as 1st and 2nd.	Ceratocombidæ (p. 368)
28 (27).—Antennæ moderate, without long hairs, 3rd and 4th joints much shorter than 1st and 2nd.	Anthocoridæ (p. 368)
29 (26).—Embolium absent or indistinct.	Capsidæ (p. 369)
30 (1).—Abdomen clothed ventrally with silvery pubescence: aquatic.	
31 (32).—Antennæ 5-jointed.	Hebridæ (p. 366)
32 (31).—Antennæ 4-jointed.	
33 (34).—Ocelli present.	Hydrometridæ (p. 366)
34 (33).—Ocelli absent.	Æpophilidæ (p. 367)

In addition to the foregoing the Polyctenidæ (p. 369) are a small, highly aberrant family parasitic on bats.

FAM. PENTATOMIDÆ (Shield Bugs).—SCUTELLUM USUALLY VERY LARGE REACHING AT LEAST TO THE BASE OF THE MEMBRANE, SOMETIMES ENTIRELY COVERING THE ABDOMEN. ANTENNÆ INSERTED ON LOWER SIDE OF HEAD, USUALLY 5-JOINTED; ROSTRUM 4-JOINTED.

The largest family of Heteroptera, over 3,700 species were listed by Lethierry and Severin (1893) and many more have been added since. Its members are readily separable from other Gymnocerata owing to the scutellum extending to the base of the membrane. Many species are remarkable for their beautiful coloration, and practically all have the property of emitting a nauseous odour which is caused by a fluid excreted through two ventral openings—one on each side of the metasternum.

The vast majority are vegetable feeders but members of the subfam. Asopinæ are chiefly predaceous, particularly upon lepidopterous larvæ. Nymphs of *Zicrona cœrulea* L. are recorded by Kershaw and Kirkaldy (1908) in China to prey upon larvæ of *Haltica cœrulea* Oliv. while the adults attack the beetle of that species. Others (ex. *Picromerus bidens* L.) appear to live on either plant or animal tissue. In temperate regions the species appear to be mainly single-brooded, the nymphs occurring in spring or early summer and the adults later—many of the latter hibernate. The eggs are usually barrel-shaped and deposited in compactly arranged masses. The nymphs are flattened and rounded in outline, their coloration is often striking and usually different from that of the adults; for observations on the metamorphoses of the family vide Morrill (1910). The life-history of *Chrysocoris stollii* Wolff, in S. China, has been briefly described by Kershaw and Kirkaldy (1908). That of the oriental *Tessaratoma papillosa* has also been followed by Kershaw (1907); the early stages are found on "logan" and "lichee" fruit trees which they apparently injure. Both sexes have the property of stridulation (p. 354) and are also able to eject an obnoxious fluid to a distance of 6–12 inches (Muir, 1907). In the later nymphs there are four pairs of dorsal abdominal odoriferous glands which atrophy in the adult, and are replaced by the usual ventral thoracic gland. Maternal instinct is exhibited in *Tectocoris lineola*, the parent resting in a brooding attitude over the eggs, and subsequently remaining for a while in close proximity to the newly hatched young (Dodd; *Trans. Ent. Soc.*, 1904). In *Acanthosoma interstinctum* L., which occurs on birch in England, etc., the female likewise manifests parental care for the eggs and young.

Certain exotic genera (*Ceratocoris* and *Elapheozygum*) exhibit a remarkable sexual dimorphism, the males having the head greatly produced in front of the eyes, forming prominent horn-like projections. Only a few members of the family occur in the British Isles and are found on various trees and shrubs. On the other hand over 200 genera are known from the Indian Empire which is evidently one of the most prolific regions of the world for these insects. Notwithstanding their abundance, Pentatomids are rarely major pests of crops. *Murgantia histrionica* Hahn, the "Harlequin Cabbage Bug" of the United States and Central America, is one of the best known and is especially partial to Cruciferæ. *Pentatoma lignata* Say is the "Conchuela" of N. America which is injurious to various plants (Fig. 358). *Nezara viridula* L. is remarkable in that it is almost world-wide in distribution.

The division of the Pentatomidæ into subfamilies is subject to much diversity of opinion; fifteen were recognized by Lethierry and Severin but the Plataspidinæ, Cydninæ, and Urostylinæ are elevated by more recent writers to the rank of separate families. For a generic monograph vide Schouteden; the catalogue by Kirkaldy (1909) gives full bibliographical references including habits and food-plants.

FAM. COREIDÆ.—ANTENNÆ 4-JOINTED, INSERTED ON THE UPPER PART OF THE SIDES OF THE HEAD; TARSI 3-JOINTED. A considerable family of, as a rule, dull coloured insects; *Serinetha* Spin. and a few other genera, however, are brightly coloured. They are very variable in form but narrower and more oblong than Pentatomidæ. The property of emitting nauseous odours is well developed, and they are stated to be more penetrating than those of the former family. Many genera exhibit extraordinary dilations of the antennæ and tibiæ but the function thereof is unknown. At least 1,400 species have been described, and Lethierry and Severin recognize no less than 29 sub-families, many of which are extra-European; the largest number of species are included in the Mictinæ. Coreidæ are all vegetable feeders and one of the best known species is the "Squash Bug" (*Anasa tristis* Deg.) which attacks Cucurbitaceous plants in N. America; *Leptocorisa varicornis* F. is an oriental pest of rice and millet. Twenty-one species occur in Britain.

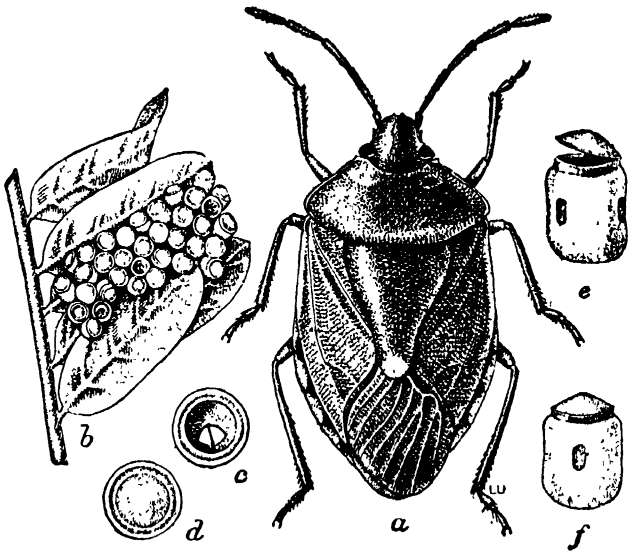

FIG. 358.—*PENTATOMA LIGNATA.*

a, imago; *b*, egg-mass; *c*, egg after hatching with operculum removed showing egg burster; *d*, egg before hatching, from above; *ef*, lateral views of egg showing operculum. All magnified. *After* Morrill, *U.S. Ent. Bull.* 64, Pt. 1 (reduced).

FAM. BERYTIDÆ.—DIFFER FROM COREIDÆ IN THE LONGER AND MORE SLENDER LEGS AND THE CLAVATE APICES TO THE FEMORA. These are delicately formed insects, never very common, and sometimes known as "stilt bugs." In habits they are sluggish, frequenting undergrowth and meadows. Although they are probably universally distributed, their small size and fragility have caused them to be overlooked, and the tropical forms have been very little collected. Eight species occur in Britain.

FAM. LYGÆIDÆ.—ANTENNÆ SITUATED BELOW A LINE DRAWN FROM THE CENTRE OF THE EYE TO THE APEX OF THE FACE. TARSI 3-JOINTED, OCELLI PRESENT. The Lygæidæ (Fig. 359) resemble the Coreidæ in general form but are usually smaller, of softer texture and often brightly coloured. All are plant feeders and mostly occur in moss, surface rubbish, beneath stones or low plants, but a few may be taken by sweeping. *Blissus leucopterus* Say is the American "Chinch Bug," which is very destructive to grasses and cereals; *Oxycarenus hyalinipennis* Costa is the Egyptian "cotton stainer" and *Nysius vinitor* Berg. is stated to be most destructive to fruit trees in Australia. Lethierry and Severin recognize 13 sub-families which include over 1,300 species; rather fewer than 70 species are British.

FAM. PYRRHOCORIDÆ (Red Bugs).—SEPARATED FROM THE LYGÆIDÆ BY THE ABSENCE OF OCELLI. A small family whose members exhibit strongly contrasting red and black coloration and include the well-known " cotton stainers " (*Dysdercus* Amy. and Serv.). The latter comprise many species, widely distributed in warm countries (Fig. 344). The name " cotton stainer " is derived from their habits of piercing the bolls and staining the fibre. *D. cingulatus* F. is a serious cotton pest in India and *D. sulphurellus* H.S. is prevalent in N. America. The widely distributed *Pyrrhocoris apterus* Fall. is the only British representative of the family, and is remarkable on account of its alary dimorphism. Muir and Kershaw (*Jour. Bombay N.H. Soc.* 1908) have followed the life-history of *Dindymus sanguineus* which is carnivorous, feeding on flies; the nymphs however, apparently prefer termites. The oriental *Lohita grandis* attains a length of over 2 in. and is sexually dimorphic, the male having the antennæ and abdomen greatly elongated.

FAM. ARADIDÆ.—BROAD FLATTENED SPECIES WITH THE HEAD PRODUCED BETWEEN THE ANTENNÆ. ABDOMEN BROADER THAN WINGS, HEMELYTRA WITH CORIUM AND MEMBRANE. ANTERIOR LEGS INSERTED ON THE MIDDLE OF THE PROSTERNUM, TARSI 2-JOINTED. All are broad flattened insects adapted to live in the narrowest of crevices, under bark, in chinks of dead trees, among fungi, etc. and are greatly compressed in the dorso-ventral plane. They are allied to the Tingidæ but are usually easily separated by the absence of reticulation. Very little is known about their habits, but oviposition differs from that which obtains in the next family, the eggs being external and not inserted into plant tissues. *Aradus* F. is world-wide in distribution with many species.

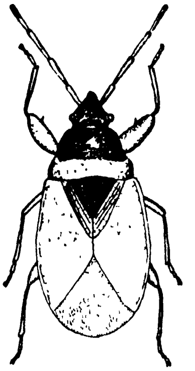

FIG. 359.—*Gastrodes ferrugineus* × 5. Britain.

FAM. TINGIDÆ (Lace Bugs).—SMALL FLATTENED INSECTS WITH THE PROTHORAX AND HEMELYTRA ADORNED WITH A CELL-LIKE PUNCTURATION OR RETICULATION. ANTERIOR LEGS INSERTED ON HIND MARGIN OF PROSTERNUM, TARSI 2-JOINTED. These attractive insects exhibit great variety of form, the prothorax often being produced into laminate outgrowths, or the whole body may be margined with closely set spines. The pronotum is also prolonged backwards so as to cover the scutellum except in *Piesma* L. & S. (which is further exceptional in possessing ocelli). In some genera there are crest-like modifications of this region suggestive of the Membracidæ. All species are plant feeders and sometimes occur in sufficient numbers to constitute minor pests. The eggs are frequently inserted upright in the plant tissue, and are invested with a brown viscid substance which hardens to form a cone-like elevation on the surface of the leaf. The immature stages are very different from the adults, the characteristic ornamentation of the latter not appearing until after the last moult. The metamorphoses of several species are known; those of *Leptobyrsa explanata* Heid. are well figured by Crosby and Hadley (*Jour. Econ. Ent.* 8). *Stephanitis* (*Tingis*) *pyri* F. attacks pear and apple in Europe, badly infested leaves dying. Species of *Copium* Thunb. are known to form galls on *Teucrium* and, according to Houard, castration of the floral generative organs results. For a monograph on the species *Piesma quadrata,* see Wille (1929).

FAM. HEBRIDÆ.—ABDOMEN CLOTHED VENTRALLY WITH SILVERY PUBESCENCE; ANTENNÆ 5-JOINTED, TARSI 2-JOINTED. A small family of minute subaquatic species found amongst Sphagnum, Lemna, etc. in marshes and other wet localities. *Hebrus* Curt. (*Naeogeus* Lap.) is widely distributed with two British species.

FAM. HYDROMETRIDÆ (Pond Skaters).—AQUATIC, CLOTHED VENTRALLY WITH SILVERY PUBESCENCE. HEMELYTRA OF UNIFORM TEXTURE UNDIVIDED INTO AREAS; ANTENNÆ 4-JOINTED. A family including some very heterogenous forms exhibiting habits of great biological interest. All are aquatic or subaquatic and mainly feed upon dead insects or those which accidentally occur floating on the surface. The ventral pubescence renders them incapable of being wetted and odoriferous sacs are absent. Both macropterous and apterous forms are frequent. *Mesovelia* Muls. and Rey. frequents the leaves of water plants and imbeds its ova in the stems thereof. For its life-history consult Hungerford (*Psyche,* 1917) and Butler (*Ent. Month. Mag.* 1893). *Hydrometra* Latr. frequents stagnant water: it is very elongate and linear with a greatly attenuated head (Fig. 360). It has the peculiar habit of crawling slowly over the surface of the water. *Velia* Latr. affects streams and is often gregarious; macropterous forms are rare and the hemelytra, when present, are entirely membranous. *Rhagovelia* swims against the current of swift streams. The last tarsal joint of its middle pair of legs has a fan-like arrangement of hairs which spreads out and functions very much after the manner of the webbed feet of water-fowl (*Bueno*). *Gerris* F. is universally distributed and readily distinguishable by its long legs and habit of jumping along the surface of the water. Its ova are stated to be deposited in a group surrounded by a kind of mucilage and attached to submerged plants: very little detailed information has been published on its metamorphosis. *Halobates* Esch. and its allies are apterous and frequent the tropical and subtropical oceans, often occurring many hundreds of miles from land. They have been observed running over the surface of the sea in calm weather and feed upon dead, floating marine animals. An account of the structure of *Halobates* is given by White (1883).

FAM. ÆPOPHILIDÆ.—SEPARATED FROM HYDROMETRIDÆ BY THE CONTIGUOUS COXÆ, VISIBLE SCUTELLUM AND ABSENCE OF OCELLI. A family including a single species *Æpophilus bonnairei* Sign. This insect has vestigial hemelytra and lives beneath stones, etc., some distance below high-tide mark on the coasts of Ireland, South England and neighbouring countries of Europe. Its biology has been studied by Lienhart (*Ann Sci. Nat.* 1913).

FAM. HENICOCEPHALIDÆ. — ROSTRUM SHORT, CURVED AT THE BASE SO AS NOT TO LIE AGAINST THE VENTRAL SURFACE. HEAD VERY LONG, CONSTRICTED BY A TRANSVERSE POST-OCULAR IMPRESSION. PRONOTUM WITH TWO TRANSVERSE CONSTRICTIONS, APPEARING TRISEGMENTED. HEMELYTRA ENTIRELY MEMBRANOUS. A very small but widely distributed family, the members of which occasionally appear in swarms like midges; such swarms have been observed in South America, Tasmania, and Ceylon. In *Ænictopechys allaudi* Jean. (Africa) the rostrum projects forwards in a manner quite different from other Hemiptera, and its apex is bifid.

FAM. PHYMATIDÆ (Macrocephalidæ).— FORE-LEGS SHORT AND VERY STOUT, WITH LONG COXÆ, SHORT THICK FEMORA, AND CURVED POINTED TIBIÆ. TARSI 2-JOINTED, SOMETIMES ABSENT. The members of this tropical family are predaceous, with the fore-legs adapted for grasping. Some of the species have the habit of secreting themselves in flowers for the purpose of securing prey which may come within reach. In the oriental genus *Carcinocoris* Handl. the whole body is margined with fine spines and the front tibia is articulated to the femur in such a manner as to form a pair of pincers. The prey of these insects consists of small members of other orders and also Tenthredinid larvæ.

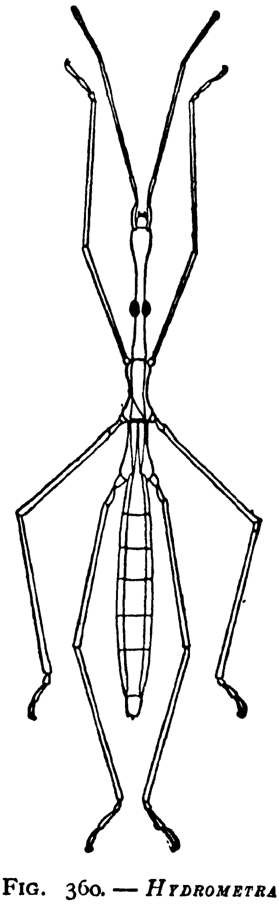

FIG. 360. — *Hydrometra stagnorum* × 8·5. Britain.

FAM. REDUVIIDÆ (including Nabidæ). — ROSTRUM SHORT, USUALLY 3-JOINTED, CURVED SO AS NOT TO LIE AGAINST THE UNDER-SURFACE OF THE HEAD WHEN IN REPOSE. OCELLI, WHEN PRESENT, PLACED BEHIND THE EYES. ANTENNÆ FILIFORM. HEMELYTRA, WHEN DEVELOPED, COMPLETE. This extensive family exhibits an extremely wide range of variation in form among various genera, such dissimilarity being scarcely paralleled in any other family of insects. Upwards of 2,000 species are known and are grouped in twelve subfamilies, of which the largest is the Harpactorinæ. By some authorities the Nabidinæ and Emesinæ are regarded as separate families. There are eighteen British species, which mostly pertain to the Nabidinæ. A large number of members of the family are predaceous and are sometimes known as "Assassin Bugs." Although usually living on the blood of other insects they occasionally attack the higher animals, including man; some species, possibly, are vegetable feeders. *Triatoma* Lap. (*Conorhinus*) includes voracious blood-suckers and is largely American. *T. megista* is the main carrier of *Trypanosoma cruzi*, the causal agent of a fatal form of human trypanosomiasis in South America. *T. rubrofasciata* Deg. also extends into Madagascar and South Asia; its nymphs are common in houses, where they are partially concealed with floor debris. It has been suggested that this species is concerned with the transmission of Kala-azar. The punctures of species of *Triatoma* cause a burning pain which may last for two to four days. According to

Cornwall and Patton the secretion from the ovoid salivary glands of *T. rubrofasciata* contains a powerful anticoagulin and is probably the source of the irritation induced. *Reduvius personatus* L. (Fig. 361) also frequents houses, normally preying upon *Cimex* and other insects; it is known to attack man, inflicting severe pain. Although uncommon in Britain it is widely distributed in Europe, and has been introduced into North America. Certain members of the large genus *Acanthaspis* Amy. & Serv. are also capable of inflicting painful punctures. Among the more exceptional members of the family is the genus *Afrodecius* Jeann., in which the third joint of the rostrum is apposible to a process on the second joint, suggesting an organ of prehension. The insect is African and resembles *Lycus* (Coleoptera) in form and coloration. *Rhaphidosoma* Amy. & Serv. is apterous and greatly attenuated, resembling Phasmids. *Arilus* (*Prionidus*) *cristatus* L. is the "Wheel Bug" of North America, which frequents fruit-trees, preying upon various soft-bodied larvæ. *Harpactor costalis* Stal. preys upon *Dysdercus cingulatus* in India, closely resembling it in coloration (Lefroy). *Nabis* Latr. and its allies differ from all other Reduviidæ in the rostrum being 4-jointed.

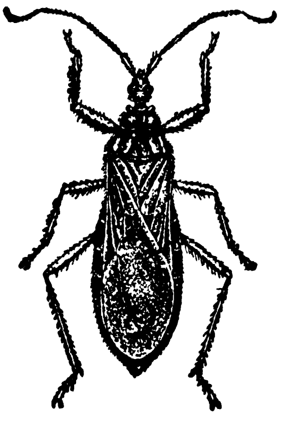

FIG. 361.—*Reduvius personatus* (ENLARGED). *After* Howard.

FAM. CIMICIDÆ (**Acanthiidæ**: Bed-bugs).—OVOID FLATTENED INSECTS WITH VERY SHORT HEMELYTRA; ROSTRUM LYING IN A VENTRAL GROOVE, OCELLI ABSENT, TARSI 3-JOINTED. PARASITES OF MAMMALS AND BIRDS. A small but well-defined family of blood-sucking ectoparasites. The bed-bugs (Fig. 362) belong to the genus *Cimex* L. (*Acanthia* F. *Clinocoris* Fall.) and the two common species are *C. lectularius* L., which is prevalent throughout Europe and N. America and is almost cosmopolitan, and *C. rotundatus* Sign. (*hemiptera* F.) which abounds in southern Asia and also in Africa. They are particularly prevalent in dirty houses, especially in large cities, and are nocturnal in habits, hiding by day in any convenient crevices about the walls, floors or furniture of rooms. Man is the host for both species, and the effect of their punctures varies very much with the individual person: with some people swelling and irritation may last for several days, with others the effects are but slight. Pathologists have suspected the bed-bug of transmitting various diseases from infected to healthy persons, but definite confirmatory evidence has usually not been forthcoming. There is evidence, however, that *C. rotundatus* may transmit bubonic plague. The eggs of bed-bugs (Fig 363) are laid in crevices, etc., of wooden bedsteads and other objects and, under favourable laboratory conditions, hatch in about eight days and the life-cycle is completed in seven weeks. Under normal conditions, however, the latter period may occupy six months and over. A fuller account of the structure and biology of these insects is given in the textbook of Patton and Cragg. Other members of the genus are parasites of birds and bats; *Œciacus hirudinis* Jen. lives in martin's nests and *Hæmatosiphon inodorus* (Duges), which occurs in North and Central America, is a pest of poultry and has a greatly elongated rostrum.

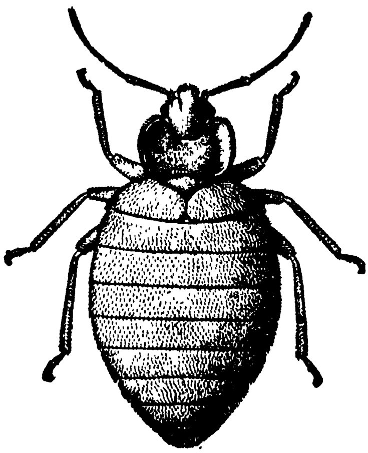

FIG. 362.—*Cimex lectularius*, MALE, × 10. EUROPE, N. AMERICA, ETC.

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FAM. CERATOCOMBIDÆ. (**Dipsocoridæ**).—HEMELYTRA WITH EMBOLIUM; ANTENNÆ LONG AND FILIFORM, HAIRY, 3RD AND 4TH JOINTS TOGETHER TWICE AS LONG AS 1ST AND 2ND. OCELLI PRESENT. A family consisting chiefly of minute species found among moss, dead leaves, etc., and related to the Cimicidæ and Anthocoridæ. The three British species of *Ceratocombidæ* are all minute and readily mistaken for small Diptera.

FAM. ANTHOCORIDÆ.—HEMELYTRA WITH EMBOLIUM; 3RD AND 4TH ANTENNAL JOINTS MUCH LESS THAN TWICE AS LONG AS 1ST AND 2ND. OCELLI PRESENT. Herewith are included small, obscure insects affecting woodlands, hedgerows, etc. The genus

Anthocoris Fall. comprises numerous closely allied species often preying upon Aphididæ. Both this genus and its allies have the rostrum 3-jointed and the tarsi 2- or 3-jointed; *A. Kingi* Brumpt (in the Sudan) and the cosmopolitan *Lectocoris campestris* F. are known to suck human blood. In *Microphysa* Westw. and *Myrmedobia* Baer the rostrum is 4-jointed and the tarsi 2-jointed; hemelytra are only developed in the male, and the female has a curiously globular, contracted abdomen. *Termatophylum* Reut. from Egypt is now regarded as constituting a separate family. About 30 species of Anthocoridæ occur in the British Isles.

FAM. POLYCTENIDÆ.—INSECTS PARASITIC UPON BATS AND PROVIDED WITH CTENIDIA. ROSTRUM 3-JOINTED, ANTENNÆ AND TARSI 4-JOINTED, EYES WANTING; HEMELYTRA SHORT, OF UNIFORM CONSISTENCY AND DEVOID OF A MEMBRANE. The genus *Polyctenes* Gigl. was originally placed in the Nycteribidæ. Westwood (1874) subsequently founded the above family for its reception as an aberrant member of the Anopleura. In 1879 Waterhouse relegated it to the Hippoboscidæ, but the following year agreed with Westwood as regards its affinities. Sharp considers there is insufficient ground for removing these parasites from the Heteroptera, and in this contention he is followed by Distant (1902-10) and Speiser (1904). The species of the family are characterized by the possession of one or more combs (ctenidia) of short flat spines —an armature which they share with *Platypsylla*, the Nycteribidæ and Aphaniptera. About 20 species are known, all are bat parasites living deep down among the fur of those animals, and have been chiefly found on *Molossus*, *Megaderma*, *Taphozous* and *Cynopterus*. They are viviparous, the embryos remaining in the ovarioles where they gradually mature. The young are born at an advanced stage but differ very considerably from the adults (Hagan, *Journ. Morph. and Physiol.*, 1931). About half a dozen genera are known and are almost exclusively tropical; for an account of the family consult Jordan (1911).

FAM. CAPSIDÆ (Miridæ).—HEMELYTRA WITH A CUNEUS BUT NO EMBOLIUM; ROSTRUM AND ANTENNÆ 4-JOINTED, TARSI 3-JOINTED. OCELLI ABSENT. A very extensive family, including for the most part fragile insects with a soft integument. It constitutes the largest palæarctic family of Heteroptera, Oshanin listing 1,066 species from that region; about 180 occur in Britain. The generic distinctions, being often indefinite, are difficult to determine, and there is great need for the accurate discrimination of the species of the family, many of which are now recognized as of economic significance. Although the majority live on plant juices the habit is not universal, a number of cases being recorded of their preying on small insects (vide Reuter, 1903). There is also evidence of change of food-plant in certain instances, species living on wild plants becoming adapted to thrive on cultivated plants. Thus *Plesiocoris rugicollis* (Fig. 193), which is known to live on *Salix* and *Alnus*, now attacks apple, black and red currants, and under experimental conditions will feed upon plum (Petherbridge and Husain, 1918). The "Tarnished Plant-bug" (*Lygus pratensis* L.) is an almost cosmopolitan pest of many economic plants and has numerous named varietal forms (Crosby and Leonard, 1914). *L. pabulinus* L. attacks potatoes, etc., and *Helopeltis theivora* Waterh. is very destructive to tea in Assam. Species of the latter genus possess a curious erect, elongate pin-like spine arising from the scutellum.

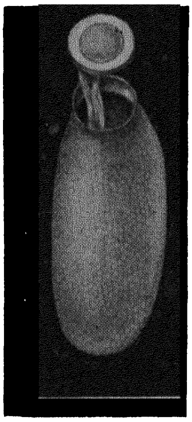

FIG. 363 — *CIMEX ROTUNDATUS*, EGG, AFTER ECLOSION OF NYMPH, SHOWING OPERCULUM: × circa 30.

FAM. SALDIDÆ (Acanthiidæ).—HEAD SHORT AND BROAD, EYES VERY LARGE AND PROMINENT WITH THE OCELLI SITUATED BETWEEN THEM. ROSTRUM LONG, 3-JOINTED, NOT APPLIED AGAINST VENTRAL SURFACE OF THE HEAD. TARSI 3-JOINTED. Most of the species frequent borders of streams and marshy places, particularly near the coast. They inhabit mud, moss or salt-marsh plants and fly and run rapidly. The large genus *Salda* F. is very widely distributed and includes 19 British species. So far as known all members of the family are predaceous (Bueno), but very few observations have been made.

FAM. HELOTREPHIDÆ.—HEAD FUSED WITH THORAX: ANTENNÆ 1- OR 2-JOINTED: NO DISTINCT VENATION. Represented by three genera of aquatic forms in the Orient and Lake Tanganyika. The fusion of the head and thorax is unique in free-living insects and the family has no close affinities with other Heteroptera.

CRYPTOCERATA (Hydrocorisæ)

Table of family characters :—

1 (4).—Body short and broad ; ocelli present.
2 (3).—Anterior legs ambulatory ; antennæ exserted. Pelogonidæ (p. 370)
3 (2).—Anterior legs prehensile ; antennæ concealed, eyes prominent. Mononychidæ (p. 370)
4 (1).—Body elongate or ovate, ocelli absent.
5 (10).—Anterior coxæ inserted near front margin of prosternum : fore-legs prehensile.
6 (9).—Antennæ 4-jointed ; no exserted respiratory appendix.
7 (8).—Posterior tibiæ spinulose. Naucoridæ (p. 370)
8 (7).—Posterior tibiæ flattened and fringed with hairs. Belostomatidæ (p. 370)
9 (6).—Antennæ 3-jointed ; abdomen with apical exserted respiratory appendix. Nepidæ (p. 371)
10 (5).—Anterior coxæ inserted near hind margin of prosternum : fore-legs not prehensile.
11 (12).—Rostrum evident, 3- or 4-jointed : front tarsi not flattened. Notonectidæ (p. 371)
12 (11).—Rostrum concealed, apparently unjointed : front tarsi flattened. Corixidæ (p. 371)

FAM. PELOGONIDÆ, FAM. MONONYCHIDÆ.—The members of these two families are much less known than other Cryptocerata and are semi-aquatic, frequenting the borders of ponds and streams. They have no British representatives, but *Pelogonus marginatus* inhabits S. Europe.

FAM. NAUCORIDÆ.—ANTENNÆ 4-JOINTED, OCELLI WANTING ; POSTERIOR TIBIÆ SLENDER AND SPINULOSE. MEMBRANE WITHOUT VEINS ; TERMINAL ABDOMINAL APPENDAGES ABSENT. A small family of moderate-sized water-bugs whose front legs are adapted for grasping and the remaining pairs for walking.

They are mostly ovoid insects of predaceous habits frequenting both fresh and stagnant water. In the oriental genus *Cheirochela* Mont. the fore-legs are very powerful and chelate. They mostly haunt aquatic vegetation, among which they creep, coming to the surface to replenish their supply of air. The latter is retained between the somewhat concave dorsum of the abdomen and the wings. The two British species belong respectively to the genera *Naucoris* Geoff. and *Aphelochirus* Westw.

FAM. BELOSTOMATIDÆ (Giant Water Bugs).—ANTENNÆ 4-JOINTED ; POSTERIOR LEGS ADAPTED FOR SWIMMING, THE TIBIÆ FLATTENED AND FRINGED WITH HAIRS. MEMBRANE RETICULATE ; ABDOMEN WITH TWO RETRACTILE APICAL APPENDAGES. In this family are included the largest members of the Heteroptera and, in fact, of almost all insects, *Lethocerus grandis* exceeding 4 in. (109 mm.) in length. They are unrepresented in Britain, but prevalent in N. America, S. Africa, and India.

In habits they are very rapacious, feeding upon small fish, tadpoles, young frogs and insects. *Lethocerus* (*Belostoma* Auct.) flies readily from one piece of water to another, is often attracted to lights and met with far away from water. The antennæ in this genus are placed in ear-like pockets on the ventral surface of the head and are not readily detected when in repose ; the 2nd to 4th joints are provided with curious curved outgrowths whose significance is unknown.

The life-history of *Belostoma* (*Zaitha*) *flumineum* has been followed by Bueno (*Canad. Ent.* 1906), and the average time taken from time of oviposition to full development is 50 days. Its favourite haunts are muddy-bottomed pools, where it lurks among the weeds. Both nymphs and adults obtain their air supply by piercing the surface film with the apex of the abdomen. The retractile appendages, when opposed, form a tube leading to the spiracles of the 6th abdominal segment (Bueno). The dorsum of the abdomen in this family is somewhat concave, forming a reservoir under the wings which is ordinarily stored with air. In *Diplonychus* Lap. and *Belostoma* Latr. the eggs are usually borne on the elytra of the males, being cemented thereto by means of a water-proof secretion. According to Slater (*Am. Nat.* 1900) they are forcibly attached to the male by the female.

FAM. NEPIDÆ (Water Scorpions).—ANTENNÆ 3-JOINTED; ANTERIOR LEGS STRONGLY PREHENSILE, POSTERIOR PAIR ADAPTED FOR WALKING; TARSI 1-JOINTED, ANTERIOR PAIR CLAWLESS. ABDOMEN WITH AN APICAL BREATHING TUBE. This family is only distantly related to other aquatic groups and its inclusion in its present position is largely one of convenience and custom. By Schiödte and Kirkaldy it is included in the Gymnocerata, the latter author placing it near the Reduviidæ. The life-history of *Ranatra quadridentata* Stål (N. America) has been followed by Bueno (1906). It occupies about 70 days from the time of oviposition to the adult stage, and the insect hibernates in the latter condition. The female is provided with a pointed toothed ovipositor, and the eggs in this genus are laid in notches cut in the petioles of water plants, each egg being provided with a pair of apical filaments. Both nymph and adults are capable of stridulation (vide Bueno, 1905). The respiratory tube is the most striking character of the family and consists of two elongate spine-like processes, each of which is grooved to form a demi-canal. Bueno finds that *Ranatra* can move the two halves of the tube at will when beneath the water, and states that they are locked together by numerous hook-like bristles. When the insect is submerged the tube penetrates the surface film and air is conducted to a pair of spiracles placed at its base. Marshall and Severin found that the insect suffered no apparent ill-effects or inconvenience after the tube had been amputated. In the immature stages the latter organ is short and is wanting in the newly hatched individual.

Nepa differs in several important characters from *Ranatra*: the respiratory tube is short and among other features the eggs (in *N. cinerea*) are deposited in chains, the ova adhering to one another by means of seven long filaments radiating from one extremity. Three pairs of "false spiracles," situated respectively on the 3rd, 4th and 5th ventral abdominal segments, are present in both *Ranatra* and *Nepa*. They are sieve-like structures with the perforations occluded by a delicate membrane, and they are also provided with sensory setæ. Baunacke (1912) has made a detailed study of their histology and regards them as exercising a static function. Bueno, on the other hand, considers that they are of a respiratory nature; he suggests that the dissolved air penetrates their closing membrane and aerates the body fluids beneath. They appear to have no direct connection with the tracheal system, and according to Martin (*Bull. Mus. Hist. Nat. Paris*, 1895) in the nymph of *Nepa* they are formed independently of the true functional spiracles of their segments. The general structure of *N. cinerea* has been studied by Hamilton (1931), but that of *Ranatra* needs further investigation, particularly in the earlier stages.

FAM. NOTONECTIDÆ.—BODY CONVEX DORSALLY; HEAD INSERTED INTO PROTHORAX, ROSTRUM 3- OR 4-JOINTED, ANTENNÆ 4-JOINTED. TARSI 2-JOINTED, ANTERIOR PAIR NOT FLATTENED, POSTERIOR PAIR DEVOID OF CLAWS. These insects differ from other aquatic Hemiptera in their habit of swimming on the back, which is shaped like the bottom of a boat. They are usually observed floating on the surface of the water with the long oar-like hind legs outstretched. They dive readily when alarmed, carrying a supply of air beneath the wings; they can also leap into the air and take to flight. Care is needed in handling them, as they are able to inflict painful punctures. *Notonecta* L. is almost universally distributed and markedly predaceous, attacking small fish, tadpoles, etc., when kept in an aquarium. In *N. glauca* (Fig. 364) the female is provided with a piercing ovipositor with which it makes incisions in the stems of water plants, partially burying an egg in each notch; certain other species merely attach their eggs to the plants. The abdomen is keeled down the middle, and arising therefrom is a longitudinal row of outwardly directed hairs on either side. These meet a corresponding series of similar hairs arising from near the pleura. In this manner there is formed a channel on either side of the abdomen, which is filled with air and enables the insect to respire when submerged. *Plea* is palæarctic and oriental and is represented in Britain by a single species *P. minutissima*; an account of the biology and external structure of this insect is given by Wefelscheid (1912).

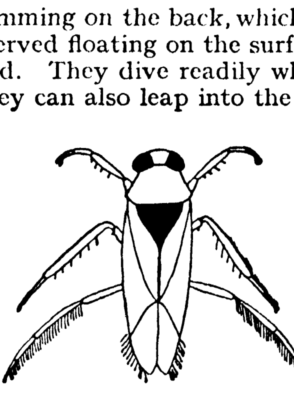

FIG. 364.—*Notonecta glauca* (enlarged). Britain.

FAM. CORIXIDÆ (Water Boatmen).—BODY FLATTENED DORSALLY; HEAD NOT INSERTED INTO THE PROTHORAX; ROSTRUM CONCEALED AND APPARENTLY UNJOINTED, ANTENNÆ 3- OR 4-JOINTED. ANTERIOR LEGS GREATLY SHORTENED, FORE AND HIND TARSI CLAWLESS, THE LATTER 2-JOINTED. The rostrum in this family is never composed of more than two joints and its peculiar structure led Borner to regard the group as a separate sub-order. The large number of species included therein implies that it is evidently the dominant family of aquatic Hemiptera. The genus *Corixa* Geoff. (Fig. 365) is nearly world-wide and includes about 30 British species.

As a rule these insects remain at the bottom of the water, holding fast by the middle legs to various objects; now and again they ascend to the surface, swiftly propelled by the hind limbs. The dorsum of the abdomen is somewhat concave, forming a reservoir beneath the wings which serves to retain a supply of air. The feeding habits of the family have been but little studied and the species may possibly be largely herbivorous. *C. geoffroyi* attaches its eggs to the stems and leaves of pond weeds by means of a glutinous substance. They are more or less onion-shaped, with one extremity prolonged into a blunt point. In some species the eggs are very numerous and closely grouped together; thus, according to Giraud, those of *C. femorata* and *mercenaria* form very considerable masses which are used as food by the Mexican Indians. Bundles of reeds are placed in the water and collected at suitable intervals, and the eggs are detached therefrom by beating the reeds. The adult insects are also used as food in Mexico and Egypt. Hagemann (1910) has contributed some observations on the respiration of *Corixa* at successive stages in its life and on the structure of the spiracles. He also describes a tympanal organ in association with the 2nd pair of the latter, which may possibly serve for the perception of stridulatory sounds produced by the male.

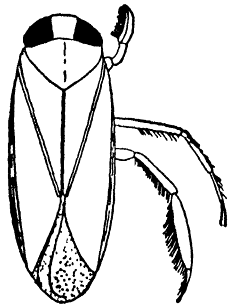

FIG. 365.—*Corixa* (ENLARGED). BRITAIN.

The minute *Micronecta* Kirk. (*Sigara*) lives in *Spongilla* and among water weeds and, like other members of the family, is able to stridulate, but this faculty is much less developed in the female than the male. The stridulatory organs of *Corixa* consist of (*a*) a strigil on the 6th abdominal tergum, which is stated to rub against the under side of the hemelytra; and (*b*) the pedal organs mentioned on p. 354.

Sub-order 2. HOMOPTERA

The chief difficulty in the taxonomy of this sub-order is the classification of the Auchenorhyncha. The various systems which have been put forward are discussed by Kirkaldy (1906) and the student is also referred to the latter author's translation of an important paper by Hansen (1900–3). In the present work Kirkaldy's later subdivision (1907) into Cicadoidea and Fulgoroidea is adopted: the former group is separable into four easily recognizable families, but the Fulgoroidea, on the other hand, include a large assemblage of divergent forms (vide Muir, *Proc. Hawaiian Ent. Soc.* 1923). Although formerly regarded as a single family, the progress of later investigation shows that the group is far too heterogeneous to admit of such relatively simple treatment. There is no general treatise on Homoptera—most works dealing with the Auchenorhyncha only. The British species (including Psyllidæ) are enumerated and figured by Edwards (1896): for the European forms Melichar's work (1896) and Sahlberg's monograph (1871) of the Scandinavian and Finnish species are important. The principal works on the Sternorhyncha are referred to under their respective families.

Series I. AUCHENORHYNCHA

The following key is largely after one kindly drawn up by the late F. Muir of Honolulu:

1 (8).—Tegulæ absent; middle coxæ short, articulations near together; hind coxæ mobile. **Cicadoidea**
2 (3).—Three ocelli near together; anterior femora thickened and

spined beneath; no empodia; male, except in a very few cases, with a sound-producing organ at the base of the abdomen. CICADIDÆ (p. 373)

3 (2).—Two ocelli only or none; empodia large.

4 (5).—Posterior coxæ short, conical, not laterally dilated; tibiæ cylindrical; flagellum composed of a large sub-pyriform base and a very slender seta. CERCOPIDÆ (p. 374)

5 (4).—Posterior coxæ transverse, dilated up to the lateral margins of the sterna; tibiæ angular; flagellum composed of numerous segments.

6 (7).—Genæ more or less dilated; loræ generally conspicuous; the frons, loræ and genæ forming one curved surface; pronotum never prolonged backwards. JASSIDÆ (p. 375)

7 (6).—Genæ not dilated; frons, loræ and genæ not forming one curved surface; pronotum generally prolonged backward into a process. MEMBRACIDÆ (p. 375)

8 (1).—Tegulæ almost always present; empodia well developed; middle coxæ elongate, articulated far apart, free and capable of lateral movement; hind coxæ immobile. **Fulgoroidea** (p. 376)

Although the term "leaf-hopper" is used more especially with reference to the Jassidæ, it is often applied to members of the other families excepting the Cicadidæ.

Super-fam. CICADOIDEA

FAM. CICADIDÆ (Cicadas).—USUALLY LARGE INSECTS WITH ENTIRELY MEMBRANOUS WINGS AND THREE SUB-CONTIGUOUS OCELLI. ANTERIOR FEMORA THICKENED AND GENERALLY SPINED BENEATH; NO EMPODIA. MALES ALMOST ALWAYS WITH A SOUND-PRODUCING APPARATUS ON EITHER SIDE OF THE BASE OF THE ABDOMEN. Their large size and sound-producing powers render these insects familiar objects in the warmer regions of the world. Considerably over 1,000 species are known, rather more than 100 being palæarctic. The only British representative is *Cicadetta montana* Scop., which occurs in the New Forest and extends as far north as Finland. The capacity for sound-production (vide p. 102) is limited to the males and varies very greatly in note and degree of intensity in different species. The sound has been variously compared to a knife-grinder, scissor-grinder, and even a railway whistle. In the moist sub-Himalayan forest tracts of India the noise emitted by these insects is almost deafening, and extremely monotonous. Notwithstanding so many species being described, their life-histories have been very little studied. The nymphs so far as known are subterranean, and the greatly enlarged and modified femora and tibiæ of the fore-legs are special adaptations to that mode of life. One of the best-known species of the family is the "periodical Cicada" (*Cicada septendecim* L.) of the United States (Figs. 366, 367), which appears in great numbers after long intervals of time. Its periodical appearance is due to the nymphs requiring thirteen (in the south) or seventeen years (in the north) for their development, and the fact that the adults of one generation appear about the same time in vast numbers. This insect has been intensively studied (Marlatt, 1907) and more than 20 distinct broods have been located in various parts of the country: the 17-year race has also been reared under field conditions from the egg. In many districts several broods of different ages are known to co-exist, thus explaining the appearance of swarms of the insect several times during the 17-year cycle. The female deposits her eggs in slits which she makes in the twigs of trees, and the young emerge in about six weeks. They fall to the ground and thereupon commence to lead a subterranean life, 12–18 inches below the surface,

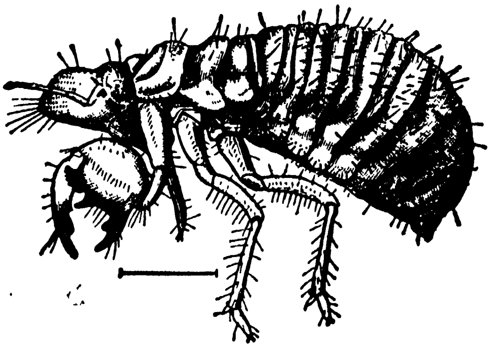

FIG. 366.—*CICADA SEPTENDECIM* NYMPH IN 4TH INSTAR.

After Marlatt. *U.S. Dept. Agric. Ent. Bull.* 71.

sucking the juices from the finer roots of various trees. In May of the 17th year they regain the surface and, leaving their nymphal exuviæ attached to tree-trunks, etc., emerge as perfect insects. When very abundant the nymphs practically honeycomb the soil, but, considering their size and numbers, the injury occasioned does not appear to be great; at times, however, fruit growers experience a good deal of loss. Under certain circumstances the final-stage nymphs (often termed pupæ) construct cones or chimneys (Fig. 367), about 4 inches high, of earthen particles wherein they live above ground for several weeks before emerging as adults. Several explanations have been offered as to the meaning of these structures and it may possibly be that in certain districts individuals prematurely reach the surface before they are prepared to become adults and construct cones as means of protection until they reach maturity. There appears to be a correlation between an unusually high local temperature and the occurrence of these cones; the latter are also stated to be prevalent over burned areas.

FAM. CERCOPIDÆ (Frog-hoppers or Cuckoo-spit insects).—OCELLI TWO OR NONE. ANTENNAL FLAGELLUM COMPOSED OF A LARGE SUB-PYRIFORM BASE AND A VERY SLENDER SETA. POSTERIOR COXÆ SHORT, CONICAL, NOT LATERALLY DILATED; TIBIÆ CYLINDRICAL, USUALLY ARMED WITH ONE OR TWO PROMINENT SPINES AND A CLUSTER OF SHORTER SPINES AT THE APEX. Members of this family may usually be separated from the Jassidæ by the characters of the tibiæ as enumerated above. Only a very few genera are palæarctic, and three thereof occur in Britain—*Triecphora* Am. and Serv., *Aphrophora* Germ., and *Philænus* Stål. The nymphs of some genera are well-known objects from their habit of establishing themselves on plants and becoming enveloped in a frothy substance commonly termed "cuckoo spit." It has been generally regarded that they are in this way protected from predaceous insects and other Arthropods, but, on the contrary, they are not infrequently seized from their spume by fossorial Hymenoptera and other enemies. Kirkaldy has observed that the froth serves to protect their soft bodies from the sun, and, when extracted from the spume and not allowed moisture, they speedily shrivel and die; probably there is truth in both explanations and the function is twofold. In adaptation to this mode of life the nymphs have to a large extent lost that power of leaping which is so characteristic of the adults, and are also nearly devoid of coloration. *Philænus spumarius* L. is the common "cuckoo spit" insect of Europe and N. America; the life-histories of this and other species of the family are described by Osborn (1916 A). It affects a wide range of wild and cultivated plants other than grasses, while *P. lineatus* L. occurs almost entirely on the latter hosts. The production of the froth has given rise to much speculation and has in recent years been studied by Sulc (1911) and Gahan (*Proc. Ent. Soc.* 1918), whose conclusions are in close agreement. According to Gahan the tergites and pleurites of the 3rd to 9th abdominal segments, instead of ending as usual at the sides to form lateral edges, are curved beneath the abdomen as membranous extensions, which meet along the mid-ventral line. Between them and the true ventral surface of the abdomen there is thus formed a cavity into which the spiracles open. This chamber is closed anteriorly, but air can be admitted or expelled by means of a posterior V-shaped valve or slit. The frothing is the result of a fluid issuing from the anus (vide p. 380) forming a film across this valve and becoming blown into bubbles by means of air expelled from the latter.

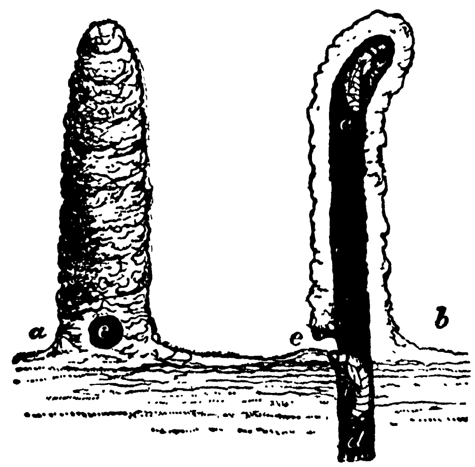

FIG. 367.—*Cicada septendecim*, "EARTHEN CHIMNEYS."

a, front view; *b*, section; *c*, nymph in last instar awaiting time of change and at *d* ready for transformation; *e*, emergence hole. From Marlatt *after* Riley.

On the 7th and 8th abdominal segments are lateral glands which have been variously interpreted. Osborn states that they secrete a viscid material which, mixing with the discharge from the alimentary canal, enables the foam to maintain its coherence, even in wet weather. Sulc and others regard the secretion as being of a waxy nature which is acted upon by an enzyme in the anal discharge. He explains that the acid thus produced forms, with the alkali present, a substance which imparts to the froth the properties of a soap-solution. In Madagascar the nymphs of *Ptyelus goudoti* are stated to discharge clear water in such amounts as to resemble fine rain. Thus Goudot estimated that some 70 individuals could emit one quart in 1½ hours. The Oriental and Australian genus *Machærota* Burm. has the scutellum prolonged backwards in the form of a relatively enormous spine thus simulating a Membracid in appearance. The nymphs of certain species of the genus are known to live in curious serpuliform tubes (about ½ in. long) attached to the branches of trees ; their life-history is figured by Lefroy (Indian Insect Life).

FAM. MEMBRACIDÆ (Tree hoppers).—GENÆ NOT DILATED ; FRONS, LORÆ AND GENÆ NOT FORMING ONE CURVED SURFACE. ANTENNAL FLAGELLUM WITH MANY JOINTS. PRONOTUM GENERALLY PROLONGED BACKWARD INTO A PROCESS ; POSTERIOR COXÆ TRANSVERSE, TIBIÆ ANGULAR. These insects may almost always be easily recognized by the pronotum, which is prolonged backwards into a prominent elevated hood or process, lying over the abdomen, and often assuming the most bizarre forms (Fig. 368). The family is most nearly related to the Jassidæ and reaches the zenith of its development in the neotropical region. The palæarctic fauna only includes three genera, two of which, *Centrotus* F. and *Gargara* Am. and Serv., are British. The eggs so far as known are deposited in small groups arranged in two nearly parallel slits cut in the twigs of trees and shrubs. The nymphal stages differ from the adults in the absence, or only partial development, of the pronotal process; the tergites are often furnished with elongate filaments or spinose projections. Certain genera (*Telamona*, *Thelia*, etc.) are affected by parasites which induce " castration parasitaire " noticeable in the reduction or other modification of the external genitalia (vide Kornhauser *Journ. Morph.* 1919). The life-history of *Vanduzea arquata* Say, a widely distributed N. American species, has been studied by Funkhauser (*Psyche*, 1915). It abounds on *Robinia* and appears to pass through two generations in the year (Ball). Both the nymphs and adults are commonly attended by ants, as is usual whenever Membracids are present in large numbers. The ants stroke the Membracids with their antennæ, whereupon the latter insects exude a liquid from a retractile anal tube. The mutual relationships of the two groups of insects has attracted the attention of a number of observers (vide Lamborn, *Trans. Ent. Soc*, 1913, p. 494). A few species have been noted to exhibit maternal solicitude ; although usually leaping away at the first alarm, they refuse to move if disturbed while guarding their offspring.

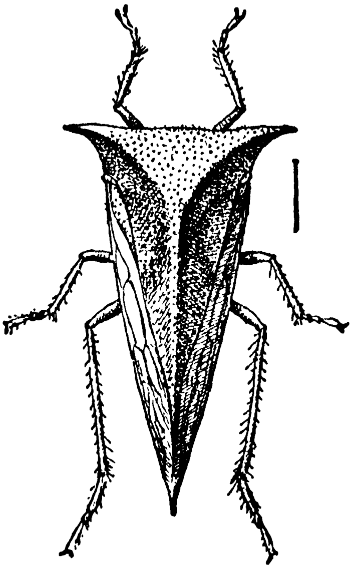

FIG. 368.—*Ceresa bubalus*, Enlarged.

After Marlatt, *Ins. Life*, 7

FAM. JASSIDÆ (Cicadellidae ; Leaf-hoppers).—OCELLI TWO, RARELY ABSENT, VARIABLE IN POSITION. ANTENNAL FLAGELLUM COMPOSED OF NUMEROUS JOINTS. GENÆ DILATED, THE FRONS, LORÆ AND GENÆ FORMING ONE CURVED SURFACE. PRONOTUM NEVER PROLONGED BACKWARDS. POSTERIOR COXÆ TRANSVERSE, LATERALLY DILATED ; TIBIÆ ANGULAR, THE HIND PAIR USUALLY SERIATELY BRISTLY, OR WITH A DOUBLE ROW OF SPINES ; EMPODIA LARGE. Excepting the Aphididæ, these insects are probably the most abundant of all Homoptera, and may be readily collected by sweeping grass, herbage and other foliage. They are slender, usually tapering posteriorly, and rest in a position ready for jumping. When disturbed they leap often several feet and readily take to the wing. Their slender form and the structure of the hind tibiæ (Fig. 369) will enable most species to be distinguished from those of the Cercopidæ. The metamorphoses of a good many are figured by Osborn (1916), that of *Idiocerus* Lewis by Leonard (*Jour. Econ. Ent.* 1915) and of *Nephotettix* by Misra (1920). The ovipositor of the female is adapted for lacerating plant-tissues ; the eggs are usually elongate and are deposited in longitudinal rows on the stems, under the leaf-sheaths, or on the leaves of the food-plant. They pass through six instars, the wing-rudiments becoming noticeable in the 3rd instar.

The species have a decided limitation of food-plant during early life but feed more indiscriminately later ; many are univoltine, others pass through two or three generations in a season. Their chief economic importance lies in their attacks upon cereal and fodder crops as well as fruit and forest trees. Thus the rice leaf-hoppers (*Nephotettix*) in 1914, were reported to have damaged 3,000,000 acres of paddy fields in one division only in the Central Provinces of India, entailing a loss of nearly £1,000,000 (Misra); similar heavy losses are recorded from the United States.

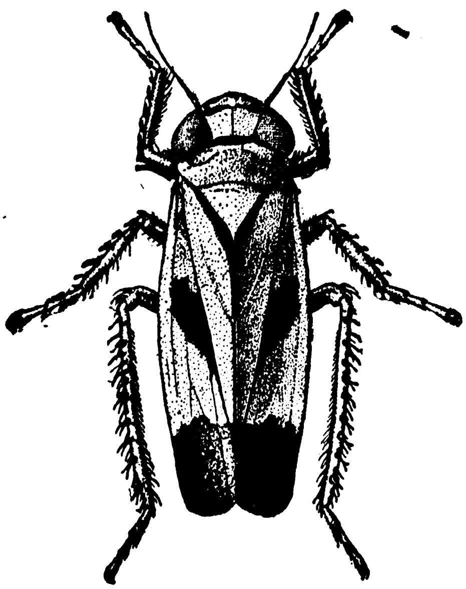

FIG. 369—*Nephotettix apicalis* × 12.
After Misra, *Mem. Dep. Agric. India Entom. Ser.* 5

In some systems of classification the Jassidæ are regarded as a superfamily and its sub-families raised to family rank. Among the more important genera are *Empoasca* Wal. which includes the Apple Leaf hopper (*E. mali.* Le B.), *Typhlocyba* Germ. (ocelli absent), *Bythoscopus* Germ. and *Deltocephalus* Burm. which includes about 100 palæarctic species.

Superfamily FULGOROIDEA

Included herewith is a large assemblage of very diverse forms whose many dissimilarities of structure render it difficult to frame any comprehensive definition. In addition to those features enumerated on p. 373 the antennæ, though very variable in form, are usually placed beneath the eyes, and the nymphs are very richly endowed with specialized sensory pits distributed over the head, wing pads and abdomen. One of the best known classifications is that of Stål whose thirteen sub-family divisions are now more usually regarded to be of family rank; alternative schemes involving a smaller number of families are discussed by Kirkaldy (1906, 1907). In a general textbook of this kind reference can only be made to the most important families, and any scheme at present proposed can only be regarded as purely tentative. Much additional morphological work is necessary before certain of the divisions can be regarded as adequately established.

FAM. FLATIDÆ.—Beautiful moth-like species, often with delicately pigmented tegmina, inhabiting tropical regions. They can usually be recognized by the well-developed transversely-veined costal cell and the granulate clavus. Both nymphs and adults frequently rest gregariously and the former are largely covered with long, curled, waxy filaments (Fig. 370). The adults of some species occur in two conspicuously different colour forms and, in the case of an African species, observed by Gregory, the insects were clustered on a stem with green individuals occupying the upper portion and red individuals situated just below them. In this attitude they were curiously like a red-flowered spike with green unopened buds above. In other dimorphic species the colour forms have been observed intermixed; for a discussion of this subject and the literature thereon vide Imms (*Proc. Manchester Phil. Soc.* 58).

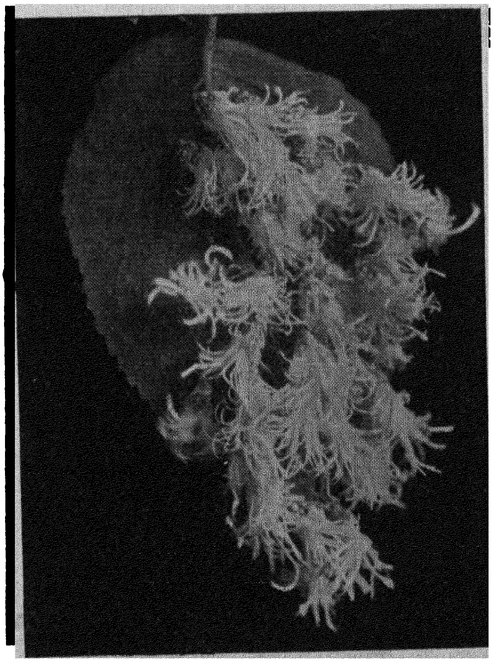

FIG. 370.—*Phromnia marginella*, INDIA: A COLONY OF NYMPHS ON A LEAF: ABOUT ⅔ ACTUAL SIZE.

FAM. DELPHACIDÆ.—One of the most characteristic features is the large, mobile, serrulate apical spur on the hind tibiæ; the costal cell is wanting and the clavus non-granulate. This family is well represented in Great Britain where there are about 70 species of which over 56 belong to the extensive genus *Liburnia* Stål. The sugar-cane leaf-hopper *Perkinsiella saccharicida* Kirk. (Fig. 371). is very destructive in Queensland and was formerly so in the Hawaiian Islands ; owing to the habit of oviposition in cane stalks this and other species are liable to transportation.

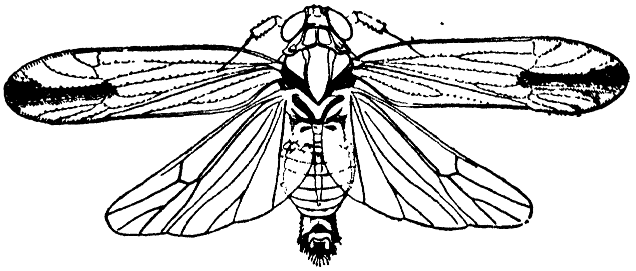

FIG. 371.—*PERKINSIELLA SACCHARICIDA*, MALE : MAGNIFIED. *After* Kirkaldy, *Entom. Bull. Pt.* 9, *Hawaiian Sugar Planters' Assn.*

FAM. FULGORIDÆ. (Lantern Flies). — Principally characterized by the reticulated anal area of the wing. A tropical family including many brilliantly coloured insects, often of large size. In many genera the front of the head is greatly drawn out to form a huge hollow proboscis-like prolongation which was, at one time, believed to be luminous. Some species have the power of secreting quantities of a flocculent white wax which, in *Phenax*, streams behind as long filaments while the insect flies.

FAM. DERBIDÆ—Very delicate, usually long-winged insects in which the anal area is not reticulated and the last joint of the labium is short. None are British.

Series II. **STERNORHYNCHA (Phytopthires)**

Table of families.

1 (2).—Tarsi 1-jointed with a single claw. Females scale-like, gall-like or covered with waxy exudation ; apterous and often devoid of legs. Males dipterous, mouth-parts atrophied. Coccidæ (p. 385)
2 (1).—Tarsi 2-jointed, basal joint sometimes reduced, with paired claws. Mouth-parts present in both sexes. Wings when present four in number.
3 (4).—Femora thickened, antennæ usually 10-jointed. Fore-wings of rather harder consistency than hind pair. Psyllidæ (p. 377)
4 (3).—Legs long, slender ; wings of equal consistency, antennæ 3- to 7-jointed.
5 (6).—Wings opaque, whitish, clouded, or mottled with spots or bands. Tarsi with 2 nearly equal joints. Aleyrodidæ (p. 378)
6 (5).—Wings transparent, tarsi 2-jointed, basal joint sometimes reduced. Paired dorsal processes usually present on 5th abdominal segment. Aphididæ (p. 380)

FAM. PSYLLIDÆ (**Chermidæ:** Jumping Plant Lice).—TARSI 2-JOINTED, ANTENNÆ USUALLY 10-JOINTED, FORE-WINGS OF FIRMER CONSISTENCY THAN HIND PAIR. Psyllids are small insects about the size of aphides and bear a resemblance to minute cicadas. They are usually very active, their rapid movements being a combination of leaping and flying, but are incapable of sustained flight. The act of leaping is performed with the aid of the hind-legs which are larger and more muscular than the other pairs. The venation is simple and exhibits relatively few marked deviations among various genera. The most striking feature in the fore-wing is the presence of a principal basal vein formed by the fusion of the stems of R,M and Cu. (Fig. 372). In *Trioza* Först. and its allies, this compound vein divides distally into its three components while in *Psylla* Geoff. and related genera it is bifurcate dividing into R and M + Cu, the latter again dividing into M and Cu. In the hind-wing the venation is extremely simple ; R is represented by Rs only, M is unforked and Cu divided into Cu_1 and Cu_2 as in the fore-wing. Cross veins are absent from both wings and A is vestigial or wanting. A general account of the external anatomy of Psyllids is given by Crawford (1914) and of the venation by Patch (1909). The chief source of information on the internal anatomy is a paper by Witlaczil (1885), and an account of the morphology of *Pachypsylla* Riley is given by Stough (1910) and of the mouth-parts of *Psylla* by Grove (1919). A general catalogue of the family is given by Aulmann (1913) ; for the British forms consult Edwards (1896) who enumerates 23 species. A very full bibliography of Psyllids is given by Zacher (*Central. Bakter.* 1916) ; many references will also be found in the work of Crawford (l.c.).

The life-history of the " Apple Sucker " *Psylla mali* Schm. (vide Speyer) may be regarded as fairly typical (Fig. 372). It passes the winter in the egg, the latter being laid about the beginning of September on the spurs of the food-plant, around leaf scars, and in cracks, etc., on the new wood. The nymphs hatch in April, and are flattened objects with whitish waxen threads projecting from the extremity of the abdomen. Five nymphal instars occur, and the different stages may be recognized by the increasing number of antennal joints; thus these organs are 2-jointed in the first instar and 7-jointed in the fifth. Wing pads are evident in the third instar and during later development they extend laterally in a prominent manner so as to make the insect appear nearly as broad as long (Fig. 372B). The imago appears in early summer and the species is univoltine. The nymphs are very injurious to the apple in Britain, damaging the blossoms and stunting the shoots; the imagines, on the other hand, cause little appreciable injury. The "Pear Sucker" *P. pyricola* Först. is very destructive in America and exhibits a different life-history. It is tri-voltine, hibernates as an imago and both nymphs and adults are injurious. The winter form of the imago differs from the summer type and was formerly regarded as a separate

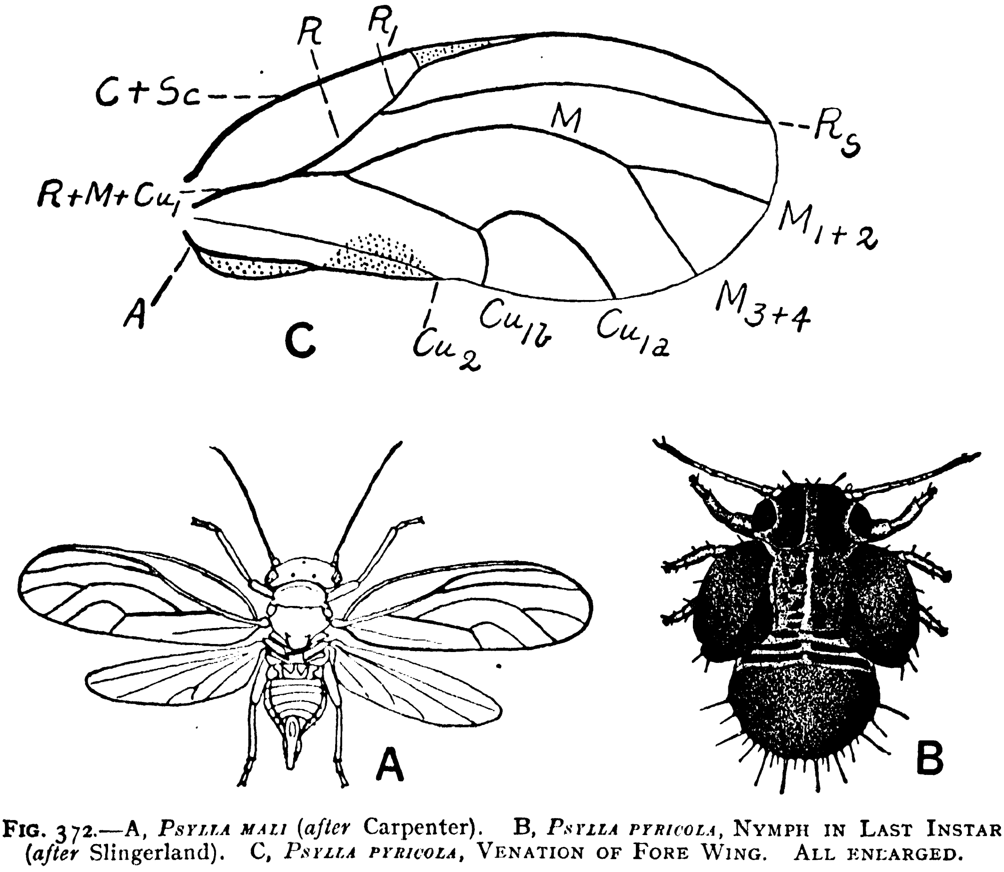

FIG. 372.—A, *Psylla mali* (*after* Carpenter). B, *Psylla pyricola*, Nymph in Last Instar (*after* Slingerland). C, *Psylla pyricola*, Venation of Fore Wing. All enlarged.

species. It is about one-third larger than the summer form and of much darker coloration, particularly with regard to the wing veins. Certain species produce gall-like malformations on their food-plants; thus in Britain *Psylla buxi* causes the apical shoots of the box to become deformed into miniature cabbage-like growths, and *Livia juncorum* Latr. forms tassel-like galls on rushes. When Psyllids are abundant copious honey-dew is excreted by the nymphs on to the leaves and twigs. In *Psylla mali* a long waxen thread enclosing a central core of translucent liquid exudes through the anus and when the threads become broken up the fluid spreads over the leaves and twigs (Awati).

FAM. ALEYRODIDÆ (Aleurodidæ : White Flies).—WINGS WHITISH, CLOUDED, OR MOTTLED WITH SPOTS OR BANDS; BODY AND WINGS MORE OR LESS MEALY. ANTENNÆ 7-JOINTED; TARSI 2-JOINTED, WITH A SPINIFORM OR SOMEWHAT PAD-LIKE EMPODIUM BETWEEN THE CLAWS. A RUDIMENTARY PUPAL INSTAR IN BOTH SEXES. The "white flies" are a much neglected group related to the Psyllidæ and probably the majority of the world's species are as yet unknown. Both sexes are winged and are dusted with a characteristic mealy white powdery wax; all are small or minute with an average wing expanse of about 3 mm. *Asterochiton* (*Aleyrodes*) *vaporariorum* Westw. is the well-known "Greenhouse white fly" which is particularly injurious to tomato and cucumber, the insect infesting the lower surface of the leaves in all its stages (Fig. 359). *Dialeurodes citri* Riley and How. is the "Citrus white fly" which is destructive to Citrus in the southern United States (Morrill and Back, 1911). The most characteristic organ of the Aleyrodidæ is the *vasiform orifice* which opens on the dorsal surface of the last abdominal segment. It is a conspicuous opening provided with an *operculum*, and situated within the orifice and beneath the operculum is a tongue- or strap-shaped organ known as the *lingula*. The latter in some species is covered by the operculum and in others it projects beyond it. The anus opens within the orifice at the base of the lingula. Honey-dew is excreted in large quantities by the insect in all stages, particularly by the larvæ. It issues through the anus accumulating on the lingula, and this fact probably gave rise to the view that the latter organ secretes the honey-dew. The vasiform orifice is present both in the larval and adult stages and, in the latter, affords characters of taxonomic value.

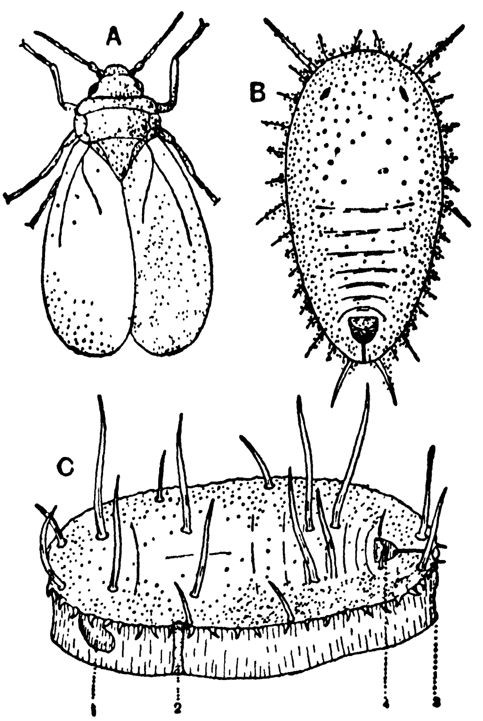

FIG. 373.—*ASTEROCHITON VAPORARIORUM.*

A, imago × 50; B, larva in first instar × 150; C, puparium × 65. 1, adult eye; 2, thoracic breathing fold; 3, caudal breathing fold; 4, vasiform orifice. *After* Lloyd, *Ann. App. Biol.* 9.

The venation shows closest affinity with the Psyllidæ (*Trioza*); it is always much reduced and exhibits evident signs of degeneration (Fig. 373). The most primitive condition is seen in *Udamoselis* End.; in other genera C and Sc are more or less fused, R_1 often disappears, and either M or Cu may be present but are usually not coexistent. With the exception of R the veins are unbranched and, in the most modified forms, practically the only remaining vein is Rs.

Parthenogenesis is a common phenomenon in several species and probably occurs in many others, but the subject needs thorough investigation. Morrill and Back (1911) observe that virgin females of *D. citri* produce males. According to Schrader (*Ann. App. Biol.* 13, 1926) in *A. vaporariorum* there are two parthenogenetic races, one of which produces males and the other females; the fertilized females give rise to individuals of both sexes.

The eggs are very characteristic, being provided with a pedicel which, in some cases, exceeds the length of the egg itself. According to Cary (1903), at the time of fertilization the lumen of the pedicel is filled with protoplasm. The spermatozoan moves through the latter until it meets the female pronucleus which migrates until it comes to lie at the entrance to the pedicel. After fertilization the contents of the pedicel shrivel up. The eggs are attached to the leaves of the food-plant by means of this stalk, and are generally laid in a circle or arc of a circle, one or more rows deep. Three larval instars are present and a so-called pupal stage. The larvæ are ovoid and greatly flattened and, after the first moult, the legs and antennæ degenerate; towards the end of the 3rd instar the imaginal organs become visible. The so-called pupal stage is only imperfectly understood: it is similar in general shape to the larva, but differs very much in appearance, being thicker and more opaque and, frequently, adorned with conspicuous rods or filaments of wax. During the first part of this instar the insect feeds after the manner of the larvæ. Towards the end of the period it becomes inactive, remaining anchored to the leaf by means of its stylets, and exhibits the characters of a rudimentary pupa with the imaginal appendages enclosed in their sheaths clearly visible within the outer case. The imago emerges by means of a T-shaped rupture of the dorsal wall of the latter. For a detailed study of *A. vaporariorum*, see the recent memoir by Weber (1931).

FAM. APHIDIDÆ (Green-fly, Plant-lice).—WINGS TRANSPARENT, ONLY FOUND

AS A RULE IN THE MALE AND CERTAIN AGAMIC FEMALES; BOTH PAIRS OF SIMILAR CONSISTENCY. TARSI 2-JOINTED, OR THE BASAL JOINT VESTIGIAL. ROSTRUM LONG, ANTENNÆ 3 TO 6-JOINTED; EMPODIA VESTIGIAL OR ABSENT. FIFTH ABDOMINAL SEGMENT GENERALLY WITH A PAIR OF DORSAL CORNICLES. These familiar insects, as a rule, pass their life on the young shoots and foliage of plants. A few species, however, live below ground on roots (ex. *Rhizobius*), some others occur on the branches of woody trees and shrubs (ex. *Lachnus*) and a certain number are gall-formers (ex. *Pemphigus, Hormaphis*). A few such as *Phylloxera vastatrix* and *Eriosoma lanigera* live both on the leaves, or shoots, and roots. The apterous generations of aphides, more especially when of flattened form (as in *Hormaphis*), are liable to confusion with the nymphs of other Sternorhyncha. Usually they may be distinguished therefrom by the following combination of characters, viz.—the 2-jointed tarsi with paired claws, the long several-jointed rostrum, the frequent presence of compound eyes and cornicles, and 9 pairs of lateral spiracles. Perhaps the most characteristic morphological features associated with these insects are the cornicles or "honey tubes"; the latter organs, however, are greatly reduced in *Eriosoma* and other genera and totally wanting in the Phylloxerinæ. Reaumur believed their function to be excretory but later observers concluded that they secreted the sweet substance known as "honey-dew." Mordwilko (1895) and others have since demonstrated the waxy nature of the secretion of the cornicles, and Horvath (1904) concluded that they are the secretory channels belonging to glands producing a waxy fluid which acts as a protection against predaceous enemies. The latter authority also observed that honey-dew is emitted through the anus, a fact which has since been well established. Many aphides also secrete a white waxy substance, either in the form of a powder dusted over the surface of the body (ex. *Hyalopterus*), or in flocculent threads (*Eriosoma, Adelges*); in either case it is the product of dermal glands (vide p. 147).

The venation of aphides has been studied in detail by Patch (1909); both the tracheæ C and Sc are absent in all forms examined and the costal area of the adult wing is strengthened by a stout vein-like structure expanding distally into a stigma. This vein channel is interpreted as representing the fusion of the main stems of all the principal veins.

Recent students of the aphides regard them as a super-family divisible into two families, viz. the Aphididæ and Phylloxeridæ. The latter includes such well-known genera as *Phylloxera* and *Adelges* and is chiefly characterized by the fact that oviparity is not confined to the sexual females but is the rule among the agamic generations also. We prefer, however, to retain the family rank for the group and regard the above divisions as sub-families.

Aphides are remarkable on account of their peculiar mode of development and the polymorphism exhibited in different generations of the same species. The associated phenomena concerning reproduction are—(1) parthenogenesis; (2) oviparity and viviparity; (3) the occurrence of generations in which the sexes are very unequally represented, males often being wanting and frequently rare. With regard to structure the phenomena are—(1) the production of totally different types of individual of the same sex either in the same or different generations; (2) the production of individuals with perfect and also atrophied mouth-parts; (3) the production of individuals of the same sex but differing as to the gonads. Associated with habits are—(1) migration to totally different plant hosts; (2) different modes of life of the same species on the same host; (3) different habits of individuals of the same generation (Parallel series).

In extreme cases almost all the above phenomena may occur associated with the annual cycle of an individual species. The most usual life-history of an aphid is as follows (Fig. 374). The winter is passed as eggs which are laid during the previous autumn by sexual females. With the advent of spring they hatch and give rise to apterous parthenogenetic viviparous females. The latter produce a new generation of similar forms among which a few winged females may occur. A variable number of generations of this kind are produced throughout the summer and winged viviparous females often become common. The latter are concerned with the migration and dispersal of the species and are produced in varying numbers in different generations. At times these winged females appear in such swarms as to darken the sky and cover the vegetation. Those individuals which are fortunate enough to find plant hosts of the right species similarly reproduce on their own account. Towards the end of summer or in the autumn their progeny, and also those of the apterous forms which remained on the original plant, give rise to sexual males and females. These latter pair and the females are oviparous, their eggs overwintering on the food-plant, and the same cycle is repeated annually. In non-migratory aphides the whole life-cycle is spent on the same plant or on individuals of the same species. If any migration to other species of host does occur it is inconsiderable and an alternation of hosts is not essential to the life of the species. Among migratory forms well-known species are—*Pemphigus bursarius* L. which occurs on poplar and flies to the roots of various Compositæ, returning to poplar in autumn. *Rhopalosiphum lactucæ* Kalt. (*ribis* Buck.) which is found on black currant in spring and migrates to *Lapsana* and *Sonchus*, returning to its primary host in autumn. *Aphis rumicis* L. which is found in autumn on the spindle tree, etc.; in May and June it flies to dock, poppies, beans, etc., returning to the spindle tree in October.

The following types of individuals, arranged in sequence, are present in the life-cycle of migratory aphides (Figs. 374, 375). (1) The *Fundatrices*; apterous, viviparous, parthenogenetic females which emerge in spring from the overwintered eggs. The sense organs, legs and antennæ are not so well developed as in succeeding apterous generations, the antennæ, for example, being shorter and may comprise a smaller number of joints. The reduction of the parts is apparently correlated with increased reproductive capacity. The eyes are often smaller, or consist of fewer facets than in the succeeding generations, and there may be differences in the cornicles. In *Drepanosiphum platanoides* Schr. the fundatrices are exceptional in being winged. (2) *Fundatrigeniæ*; apterous, parthenogenetic, viviparous females which are the progeny of the fundatrices and live on the primary host. (3) *Migrantes*; these usually develop in the second, third or later generations of fundatrigeniæ and consist of winged parthenogenetic viviparous females. They develop on the primary host and subsequently fly to the secondary host. In *Drepanosiphum platanoides* all the viviparous females are winged and consequently fundatrigeniæ are wanting. (4) *Alienicolæ*; parthenogenetic, viviparous females developing for the most part on the secondary host. They often differ markedly from the fundatrices and migrantes; many generations may be produced comprising both apterous and winged forms. (5) *Sexuparæ*; parthenogenetic viviparous females which usually develop on the secondary host, the alate forms migrating to the primary host at the end of the summer. The sexuparæ terminate the generations of alienicolæ by giving rise to the sexuales. (6) *Sexuales*; usually appear but once in the life-cycle and consist of sexually reproducing males and females, the latter being oviparous. The females with rare exceptions (*Neophyllaphis* Takah., *Tamalia* Bak., *Cervaphis* Van der Goot.) are apterous, and distinguishable from the apterous viviparous generations of the same sex by the thickened tibiæ of the hind-legs, and the greater body length. The males are either winged or apterous, and in *Aphis mali* and *Chaitophorus populi* both types are produced. Intermediates between alate and apterous forms also occur. The sexuales exhibit various types of specialization among different genera, which reach their culminating point in *Eriosoma* and its allies. In these instances both sexes are apterous, there are no functional mouth-parts, the digestive system is degenerate, and the female lays only a single very large egg produced in a single ovary, the counterpart of the latter having atrophied (Baker 1915). The eggs are laid on the primary host and in this stage the vast majority of species hibernate. In *Trama*, however, the adult fundatrices may overwinter; in *Phylloxera vastatrix* the young nymphs hibernate on the vine roots and *Chermes* also passes the winter in the same stage on intermediate hosts.

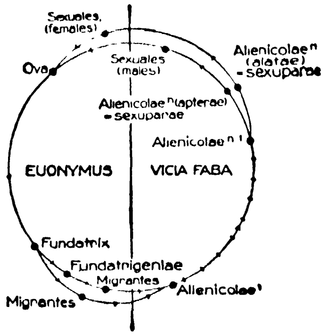

FIG. 374.—DIAGRAM OF THE LIFE-CYCLE OF *APHIS RUMICIS* (Based on observations by J. Davidson, at Rothamsted).

With non-migratory species the terms migrantes and alienicolæ are not applicable. In these cases the winged and wingless viviparous females are more conveniently referred to as fundatrigeniæ alatæ or apteræ as the case may be, and either one or the other may give rise to the sexuparæ.

We may now briefly consider the life-cycles of several species which exemplify different types of heterogeny. A high degree of specialization is met with in *Hormaphis* Ost. Sac. and the allied genera *Hamamelistes* Schim. (*Tetraphis* Horv.), and *Cerataphis* Licht. They are gall-formers not only on the primary host, but often on the secondary one also; cornicles are vestigial or wanting and the sexuales are usually small and apterous. The alienicolæ are flattened and scale-like, often with a marginal fringe of wax glands, which imparts to them a close resemblance to an aleyrodid. The life-history may become greatly abbreviated, and both the intermediate host and the aleyrodiform generations thereon eliminated, as in *Hormaphis*

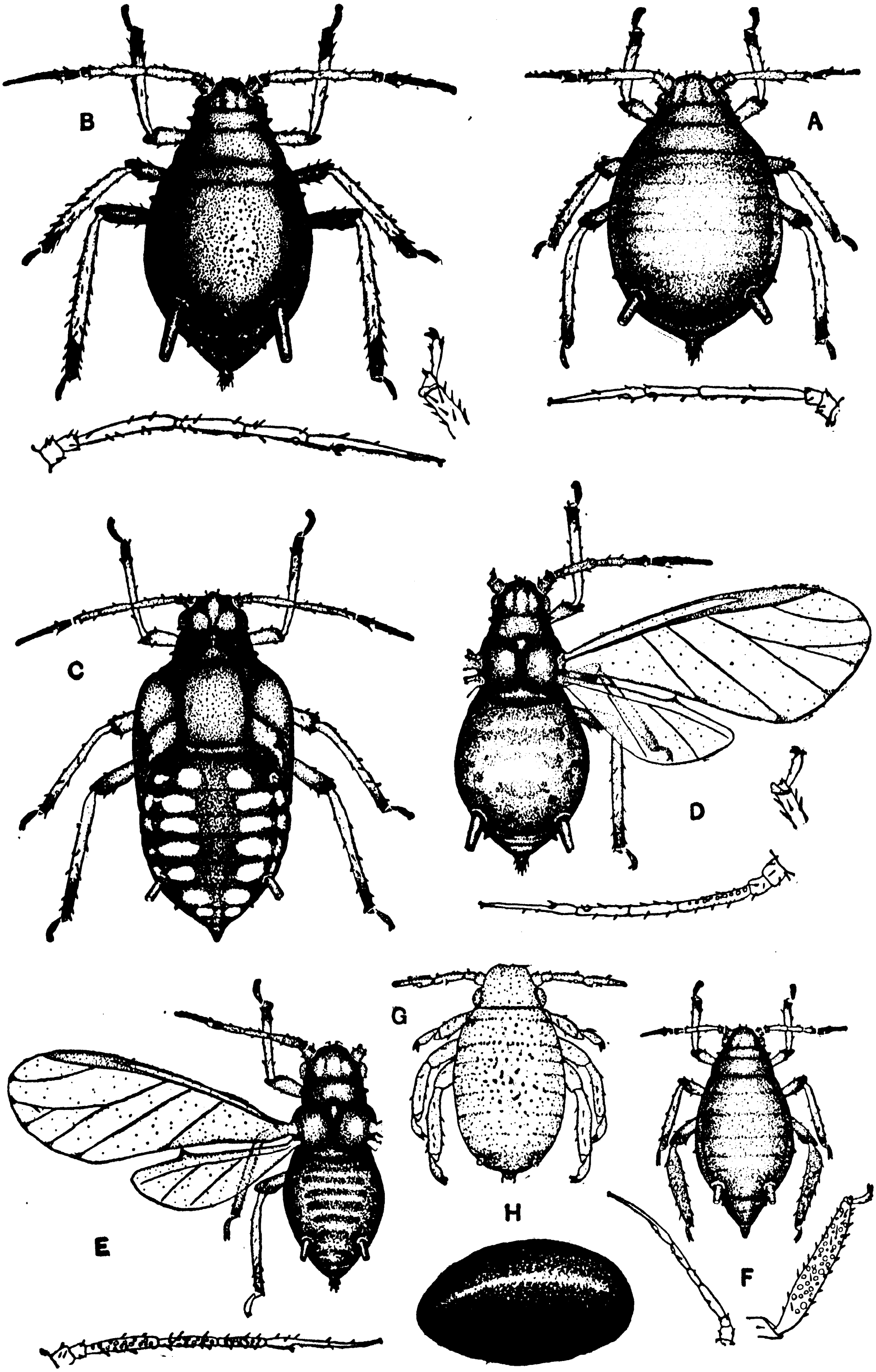

FIG. 375.—*APHIS RUMICIS.*

A, fundatrix; *B*, apterous viviparous female; *C*, nymph of winged viviparous female; *D*, winged viviparous female; *E*, male; *F*, oviparous female; *G*, fundatrix, 1st instar; *H*, egg. The antennæ are also shown under higher magnification, together with the tarsus in B and D and the hind tibia and tarsus in F. (From original drawings by J. Davidson.)

hamamelidis Ost. Sac.. According to Morgan and Shull (*Ann. Ent. Soc. Am.* 1910), in the vicinity of New York this species has only fundatrices, sexuparæ and sexuales generations.

Among the Phylloxerinæ the life-history attains the highest degree of complexity, and in *Phylloxera quercus* Lichtenstein states that no less than twenty-one forms occur in the life-cycle. In *P. vastatrix* of the vine the life-history, in a summarized form, is as follows according to Grassi (1915). The fundatrices are seldom met with on the European vine, and their fate on that plant has not been definitely settled. Grassi states that they usually perish, while those on the American vine produce leaf-galls; in no case do they develop on the roots as was formerly maintained. Given a suitable race of vine the fundatrices, therefore, are *gallicolæ* or leaf-gall formers. They lay a large number of eggs and their progeny, or fundatrigeniæ, are dimorphic when newly hatched. Grassi recognizes *neogallicolæ-gallicolæ* or those which will become gallicolæ and *neogallicolæ-radicolæ* or those which pass to the roots and become *radicolæ*. The neogallicolæ-gallicolæ pass through several generations producing in each case both gallicolæ and radicolæ. The former appear in greater numbers when the vine is in active growth and never develop on the roots. The radicolæ are produced from the later eggs when the season is advanced. They may continue as radicolæ and hibernate as nymphs, or produce sexuparæ. The latter are winged and fly to the aerial parts of the vine to lay their eggs, which are of two kinds,—the larger being female-producing and the smaller giving rise to males. The sexuales are small and apterous ; the females each lay a single large overwintering egg, on the bark of the trunk and branches, which hatches the following year into a fundatrix. The actual details of the life-cycle on the European vine in southern Europe has been productive of much discussion, but it seems probable, from Grassi's account, that the radicolæ are the principal form of the species on that host, and that gallicolæ are seldom met with. When, however, European vines are in contact with heavily galled American plants, it is stated that they are sometimes infected with neogallicolæ-gallicolæ derived from the latter. In recent years Börner has put forward the belief that the Lorraine race is a different one, which he denominates *pervastatrix*. In that province he states that the sexuales select the European vine for oviposition in preference to the American, which is usually found covered with galls in southern Europe. Similarly winter eggs were only found on the European vine and galls developed.

Related to *Phylloxera* are the genera *Adelges* (*Chermes*), *Cnaphalodes*, etc., which are confined to Coniferæ. Two hosts are normally required for the life-cycle which extends over two years ; the primary host is *Picea*, while the secondary one is either *Larix*, *Pinus*, *Abies*, or *Pseudotsuga* (Fig. 376). The life-histories of these insects are complex and very difficult to elucidate ; furthermore, it is probable that separate specific names have been applied to different cycles of the same species. For example, *Adelges viridis* (Ratz) has a cycle of five generations on spruce and larch, and the closely allied but exclusively parthenogenetic species *A. abietis* Kalt., has but two generations, both on spruce. These are regarded as distinct species by Cholodkovsky, but Börner considers that they constitute the single species *A. abietis* L. In a similar manner Börner disagrees with Cholodkovsky and unites *Cnaphalodes strobilobius* (Kalt.) and *Cnaphalodes lapponicus* Chol. into a single species under the former name. In 1909 Cholodkovsky maintained that there is a third species of *Adelges* (*A. Occidentalis* Chol.) which probably combines the reproduction cycles of both *viridis* and *abietis* but, unlike them, is confined to western Europe. Steven, however, finds that in Britain all three species are present in localities where spruce and larch grow side by side. It will be gathered, therefore, from the foregoing remarks that further research alone will determine whether several species occur, or only biological races of a single species. The principal features in the life-cycle may be summarized as follows—(1) The sexually produced eggs hatch in autumn and the first stage nymph hibernates on spruce. (2) *Fundatrices* develop from these nymphs during the following spring and their feeding habits initiate gall-formation on the primary host. They lay numerous eggs which develop within the galls and give rise to *gallicolæ*. (3) The latter issue from the galls and are divisible into winged *gallicolæ migrantes* (migrantes), which fly to the intermediate host, and *gallicolæ non-migrantes* which remain on the spruce and give rise to further fundatrices. (4) The progeny of the gallicolæ migrantes hibernate as first stage larvæ, and in the spring develop into *colonici* (alienicolæ). The colonici lay their eggs on the intermediate host; their progeny varies in type and behaviour among different genera. Thus, there may be *sistentes* which are similar to the original colonici and are apterous; other apterous forms termed *progredientes*; and *alatæ* which are akin to the latter in behaviour. (6) The *sistentes* produce among their progeny *sexuparæ* which fly to the primary host and lay their eggs thereon. (7) The apterous *sexuales* develop from the latter, and the females each lay a single egg which hatches in autumn, and thus completes the two years' cycle.

The phenomena underlying the migration of aphides are very little understood, but the main factor appears to be those physiological changes in the plant during

SCHEMATIC SUMMARY OF THE LIFE-CYCLE OF ADELGES

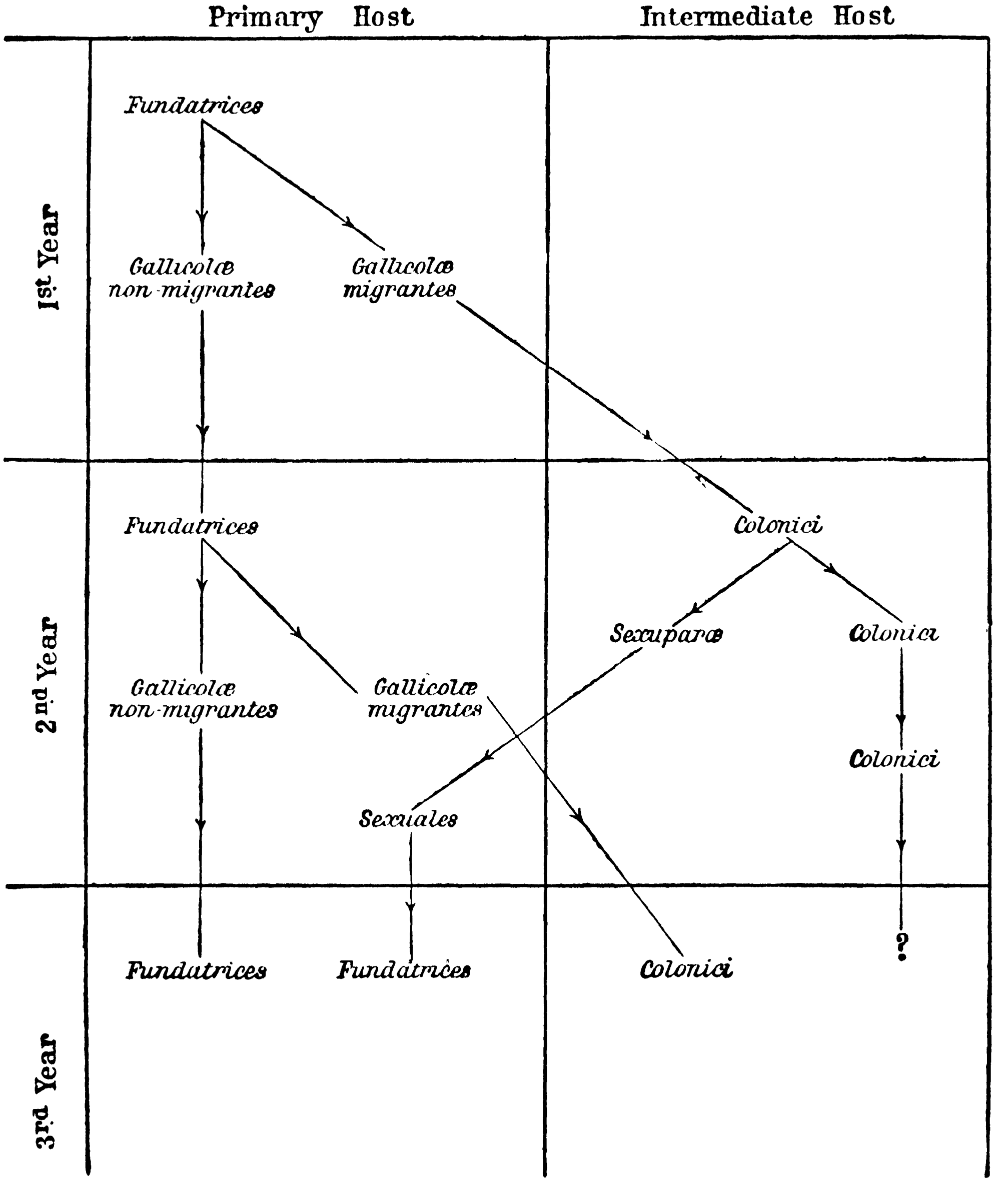

FIG. 376.

growth which render it unsuitable as a host for the aphides concerned. A reduction in the reproductive capacity of the parthenogenetic females becomes evident, and the individuals produced in each generation often become progressively smaller. The apterous individuals produce migrantes in increasing numbers and eventually the primary host becomes freed. Migrantes have been observed to appear in great numbers when the host plant wilts, or when much overcrowded with apterous forms. Moisture and temperature are additional factors, but the exact part played by them needs critical examination. Mordwilko considers that all aphides were originally polyphagous and that existing migrations are remnants of that habit. He divides these insects into three groups. (*a*) Those in which migration is absent but the species are widely polyphagous. (*b*) Species in which there is facultative migration, two hosts may be utilized and polyphagia is more restricted. Thus, a species may complete its life-cycle on one host but, on the other hand, it is capable of utilizing an alternative host for a portion of its development. (*c*) Species in which migration is obligatory and which are only slightly polyphagous.

The reproductive capacity of aphides is greatly influenced by temperature and the physiological condition of the host plant. Evidence indicates that an abundance of healthy plants coupled with a sufficiently high temperature afford conditions favourable for prolific agamic reproduction. On the other hand, these same conditions have been stated to retard the appearance of the sexuales. Kyber in 1815 bred *Macrosiphum rosæ* for four years indoors and only parthenogenetic forms resulted, although, out of doors, sexuales appeared annually. These observations appear to be supported by those of Russell (*U.S. Dept. Agric. Bull.* 90) who found that this species reproduces by parthenogenesis through the year in California.

It must, however, be borne in mind that, although the view that external factors regulate the reproductive method has received wide support, it is difficult to believe that they are actually determinative. The cytological work of Tannreuther, Morgan, Stevens and others indicates the internal or germinal factors are directly concerned in the appearance of agamic and sexual generations. It is evident that in most species there is an inherited tendency for sexual forms to be produced in autumn, but in some cases experimental evidence shows that under a favourable temperature the appearance of sexuales is prevented and agamic reproduction only occurs. In these instances temperature may possibly exercise an influence on the behaviour of the chromosomes, which in themselves are the real factors determining whether a generation be sexual or agamic.

The remarkable reproductive powers of these insects has already been referred to (p. 346) and the capacity of different species in this respect varies within very wide limits. Numerical evidence of the fecundity of *Aphis malifoliæ* Fitch is afforded by Baker and Turner (1916). The fundatrix produces on an average 71 young. From 5 to 7 generations of spring forms occur and consist at first exclusively of fundatrigeniæ, but migrantes appear in increasing numbers in each generation. The average number of young produced by the fundatrigeniæ was 121 per female: the later generations were rather less prolific. The migrantes yielded on an average 18 young per female, the alienicolæ 65, sexuparæ 7, and the sexuales produced an average of 6 eggs per female. It can be readily imagined that if this numerous progeny survived, the available supply of plant life would speedily become exhausted. This result is avoided owing to the fact that aphides are destroyed by very numerous parasitic Hymenoptera, they also form the food supply for the progeny of many Aculeata and are further preyed upon by great numbers of Coccinellidæ and larval Syrphidæ and Neuroptera. In addition to the above enemies, vast numbers are washed away by rains, and many migratory forms probably perish through failing to reach suitable hosts. In spite of all these and other controlling agencies, sufficient numbers survive to render many species pests of prime importance to the agriculturist and fruit-grower.

The literature on the family is very extensive; the monographs on the British species are those of Buckton (1876–83) and Theobald (1926–29). The work of Van der Goot (1915) on the Dutch forms includes most British species, and the monographs of Kaltenbach (1843), Koch (1854–57), and Tullgren (1909) are important to the systematist. For the classification and world genera consult Baker (1920), and for a list of species and their plant-hosts vide Patch (1912–19) and Wilson and Vickery (1918). The biology of the family has been extensively studied by Mordwilko (1907, 1909), and for information on the anatomy reference should be made to the papers by Witlaczil (1882), Mordwilko (1895), Davidson (1913, 1914) and Baker (1915). For the life-history and biology of individual species the following writings, among others, may be mentioned: Davis (1914) on *Callipterus* and (1915) on *Macrosiphum*; Patch (1913) on *Eriosoma*; Matheson (1919), Baker and Turner (1916) on species of *Aphis*; Balbiani (1884) and Grassi (1915) on *Phylloxera*; and Chrystal (*Forestry Comm. Bull.* 4, 1922) on *Adelges*, which includes a bibliography of that genus.

FAM. COCCIDÆ (Scale-insects, Mealy-bugs). TARSI 1-JOINTED WITH A SINGLE CLAW; ROSTRUM SHORT. FEMALES USUALLY DEGENERATE; SCALE-LIKE, GALL-LIKE OR WITH A POWDERY OR WAXY COATING; APTEROUS, OBSCURELY SEGMENTED, LEGS

AND ANTENNÆ OFTEN VESTIGIAL OR ATROPHIED. MALES WITH ANTERIOR WINGS ONLY, OR SOMETIMES APTEROUS; MOUTH-PARTS WANTING.

This family in some respects is one of the most anomalous of all insects. Not only is there a remarkable variety of forms within its limits, but also the sexes in the same species differ as much in characters and metamorphosis as insects pertaining to different orders. The form most usually met with is the female, and consequently the popular expressions "scale-insects" and "mealy-bugs" refer more particularly to that sex. Coccidæ are among the most important pests of cultivated plants, particularly of fruit trees, and mention need only be made of the San José Scale (*Aspidiotus perniciosus* Comst.), the Mussel Scale (*Lepidosaphes ulmi* L.) of the apple, and the Fluted Scale (*Icerya purchasi* Mask.) of citrus fruits, to establish this fact. The plant hosts are extremely numerous (vide Green, 1917–19) and probably include representatives of every natural order of Phanerogams.

Their habits, however, are very variable, some species being confined to a single food-plant; thus *Cryptococcus fagi* is only found on *Fagus sylvatica* and *Physokermes abietis* on *Abies excelsa*. On the other hand *Lepidosaphes ulmi* L. is known to infest about 130 different species of plants pertaining to widely divergent orders. The species of *Pseudococcus* Westw. (*Dactylopius* Targ.) are also very general feeders and occur on a great variety of plants grown under glass. The facility with which the living insects can be transported over long distances, along with their hosts, has resulted in many species becoming almost cosmopolitan. The strictest legislative measures are in vogue in many countries in order to guard against their further dissemination.

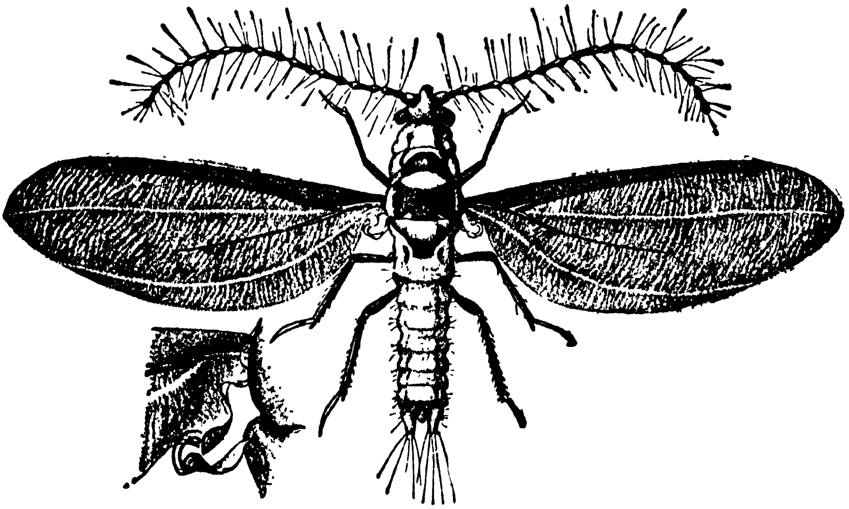

FIG. 377.—*Icerya purchasi*, MALE, ENLARGED: ON LEFT, WING POCKET AND HOOKS MORE HIGHLY MAGNIFIED.

After Riley, *Ins. Life*, I.

The males have only a single pair of wings (Fig. 377) with greatly reduced venation. In *Pseudococcus* Westw., for example, R is single-branched and only a spur-like rudiment of Sc and a portion of M are present. The hind-wings are represented by a pair of slender halteres which develop from the metathoracic wing-buds (Witlaczil); each is furnished with one or more hooklets which fit in a pocket on the wing of its side.

In a few Diaspinæ apterous males occur, while in *Chionaspis salicis* L. both apterous and winged individuals are present. In *Tachardia lacca* Kerr the males exhibit alternation of generations combined with dimorphism (Imms and Chatterjee). Thus in the first generation both apterous and winged forms are prevalent, while the second generation consists of the former only. In the majority of species the males possess four large ocelli, two being dorsal and two ventral; in such cases the compound eyes are reduced to small colourless tubercles or are totally absent. In the sub-families Monophlebinæ, Margarodinæ, and Ortheziinæ well-formed compound eyes are present, while the ocelli are either very small or wanting. The antennæ are normally 10-jointed and the mouth-parts are completely wanting, atrophy taking place during metamorphosis.

The abdomen is 8-segmented and terminated by a prominent, spine-like genital sheath which encloses the ædeagus. It is frequently accompanied by two or sometimes four (*Phenacoccus* Ckll.) or more (*Xylococcus*) long, white, filiform processes. In *Monophlebus* Burm. the conspicuous genital sheath is not evident and the somewhat truncated apex of the abdomen is furnished with 2 to 10 elongate, fleshy outgrowths. The males are always smaller than the females, and have an average wing-expanse of 2 to 4 mm.; the disparity in size of the two sexes is often extraordinarily great as, for example, in *Coccus* (*Lecanium*) *capreæ*.

The adult females are invariably apterous and usually exhibit considerable degeneration. They are always invested with some kind of specialized covering or secretory material. In *Monophlebus* Burm., *Icerya* Sign. and *Pseudococcus* Westw., etc., there is a coating of mealy substance, *Tachardia* is enclosed in a dense cell of resin-like matter, *Ceroplastes* is invested with plates of wax, while in species of *Coccus* (*Lecanium*) the hardened dorsal surface is produced by simple cuticular thickening. In the Diaspinæ a definite scale (erroneously termed a puparium) is present, it being formed either of larval exuviæ, or the latter combined with secretory material. The first larval exuviæ persist and are followed by the second, and further growth of the insect is accompanied by the formation of a secretory covering, either around the larval exuviæ, as in *Aspidiotus* Bouché, or extending behind the latter, as in *Chionaspis* Ckll. (Fig. 378). The least modified type of female is exhibited in the Monophlebinæ and Dactylopinæ. In these subfamilies the legs and antennæ are prominent, the insects retaining the power of free locomotion. Among the Coccinæ (Lecaniinæ) the legs and antennæ are frequently present in a well-developed condition, but are no longer functional, as the insect takes up a permanent position on its host after the final moult.

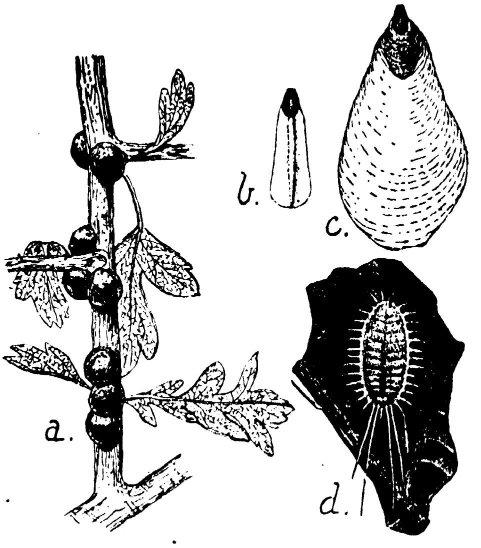

FIG. 378.—A, *COCCUS* (*LECANIUM*) *CAPREÆ* on *CRATÆGUS* (ORIGINAL): B, MALE AND C, FEMALE SCALES OF *CHIONASPIS SALICIS* (*after* Green); D, *PSEUDOCOCCUS* (*DACTYLOPIUS*), FEMALE (*after* COMSTOCK).

In the Diaspinæ the legs have totally disappeared and the antennæ are reduced to minute papillæ. A still further stage in degeneration is met with in *Physokermes*, where the insect is reduced to the condition of a sac-like object devoid of any vestiges of antennæ or legs. It is therefore evident that, if a sufficiently extensive series of genera be examined, almost every stage in transition will be found, from well-developed legs and 11-jointed antennæ to the complete disappearance of these organs. The legs, when fully formed, have 1-jointed tarsi terminated by a single claw; in a few exceptional genera the anterior tarsi are 2-jointed. Eyes may be present or absent, but are never highly developed and are often very rudimentary, as in the Diaspinæ. In the latter sub-family the abdomen calls for special mention, and is terminated by a flattened region or *pygidium*, composed of several fused segments. On its dorsal side the pygidium carries the anus and ventrally the genital aperture. On the dorsal aspect there are also numerous structures known as the tubular spinnerets, which are concerned with the secretion of the scale, but are not exclusively confined to the pygidium. Berlese (1893–95) has shown that the underlying glands communicate by long slender ducts with the capitate extremities of the tubular spinnerets.

On the ventral aspect of the pygidium, and disposed around the genital pore, are the openings of several groups (usually five) of circumgenital glands. Green has directed attention to the possible connection between these glands and oviposition. Thus in those species which are ovoviviparous the glands, as a rule, are wanting, while they are present in all oviparous species. The pores of the glands in the living insect are usually obscured by the waxy powder which they secrete, and the same powder is found dusted over the eggs. Smaller groups of similar glands occur in relation to the channels which lead from the ventral spiracles to the outer margin of the insect. They likewise produce a powdery secretion which may possibly function in excluding the entry of water, while freely admitting air to the respiratory system.

The number of eggs laid is subject to wide variation among different Coccids. In the British species it varies from about 37 in *Lepidosaphes ulmi* to nearly 2,000 in *Coccus capreæ*. They are never deposited openly on the host plant, some means of protection always being provided. Thus in the Diaspinæ they are laid beneath the scale while in *Coccus* the dried body of the female functions as an ovisac. *Orthezia* Bosc. carries them between the long waxen plates at the extremity of the body. Other genera deposit them in ovisacs of white cottony or felted waxy material secreted beneath the parent. Both oviparous and ovoviviparous species are frequent and may occur in the same genus : in the latter forms the eggs remain within the body of the parent until the contained insects emerge, or emergence may take place during oviposition.

The young larvæ are oval and flattened (Fig. 379) ; the sexes are very rarely distinguishable at this stage and it is often impossible to separate larvæ of allied genera.

Stictococcus dimorphus Newst. is exceptional in that there is well-marked sexual dimorphism in the first instar larvæ (*Bull. Ent. Res.* 1, p. 65). After the first moult the larvæ of both sexes bear a closer resemblance to the adult female, and the latter sex usually becomes mature after the second moult. On the other hand at this stage the male becomes a pupa (Fig. 379,B), with the sheaths of the imaginal appendages free, and after a third moult the adult male appears. In the Diaspinæ the scale covering the male pupa is readily recognisable by its smaller size and usually more elongate form than the female scales. It is characterized by being formed of the first exuviæ only, its complete formation taking place by the addition of secretory material during the second larval instar. *Xylococcus alni* Og. appears to be exceptional in passing through four instars in the female and five in the male (Oguma), but further research on the number of instars and other features in the metamorphosis of Coccidæ is greatly needed. In *Margarodes* Guild. the female encysts for a lengthy period accompanied by histolysis. Judging by its morphology and by the number of moults passed through the female Coccid appears to represent the pupal stage of the male and may possibly be regarded as a neoteinic form.

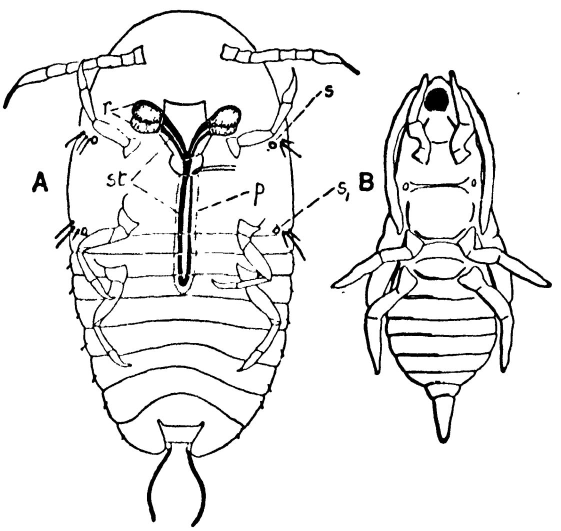

FIG. 379.—A, LARVA OF *COCCUS HESPERIDUM*, VENTRAL VIEW × 110.

p, stylet sheath ; *r*, retort-shaped organs ; *s*, s_1, spiracles ; *st*, stylets.

B, MALE PUPA OF *LEPIDOSAPHES FULVA*, VENTRAL VIEW × 48.

Adapted from Berlese, *Riv. di. Pat. Veg.*, 1893-5.

In many species fertilization is apparently the rule, and it is known in a few instances that one male may fertilize several females ; Oguma has observed that a female may also be fertilized by successive males. In other cases males are either unknown or so infrequent that parthenogenesis is evidently a common phenomenon. Thus in *Lepidosaphes ulmi* L. males are unknown on its commonest host (apple) and have only been observed on one or two less frequently infested plants.

The indigenous British Coccids are univoltine, but this rule does not apply to tropical forms or species living under glass. *Tachardia lacca*, for example, passes through two generations in the year and the San José Scale has several broods. On the other hand, Oguma states that *Xylococcus alni* requires 2½ years to complete its life-cycle.

Certain species are subterranean, particularly those of *Margarodes* and *Ripersia*, which live on the roots of plants in association with ants. A number of Coccids frequent habitations of the latter and most probably secrete honey-dew, thus rendering them acceptable guests. The honey-dew is a clear glutinous substance which is particularly attractive to Hymenoptera. It is rarely secreted by the Diaspinæ and is more especially characteristic of the Coccinæ and Dactylopinæ. Certain species are gall-formers, more especially those belonging to the Australian genus *Apiomorpha*, Rubs. (*Brachyscelis* Sch.), and the English *Eriococcus devoniensis* (Gr.), which causes gall-like deformations of the young shoots of *Erica*.

In some instances Coccids or their products have proved of considerable commercial value. Thus the "cochineal insect" (*Dactylopius coccus*), a native of Mexico living on various Cactaceæ, yields the dyestuff known as cochineal, which is prepared from the dried females. Similarly, the dyestuff known as Kermes or "*granum tinctorium*" has been used almost from time immemorial; it is likewise prepared from the dried females of *Kermes ilicis* (L.). The stick-lac of commerce from which shellac is prepared is the resinous substance formed by *Tachardia lacca* (Fig. 380). The latter insect is a native of India, where it lives on many kinds of trees, notably *Butea frondosa, Shorea robusta, Acacia arabica, Schleicheria trijuga*, and on species of *Zizyphus* and *Ficus*. The crimson colouring agent known as "lac dye" is also yielded by the bodies of the females; for an account of this insect vide Imms and Chatterjee (1915). The gum-lac insect (*Gascardia*) of Madagascar yields an inferior type of lac containing a much higher proportion of wax. Several Coccids yield wax in sufficient quantities to have been used commercially, notably the Chinese wax insect *Ericerus pe-la*, and an Indian species of *Ceroplastes*. Mention should also be made of the so-called "ground pearls," which are the outer pearly coverings of *Margarodes*. These are collected and strung into necklaces particularly in S. Africa and the Bahamas.

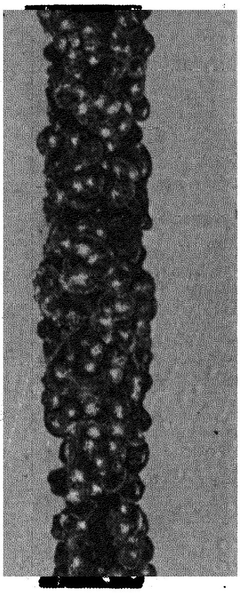

FIG. 380.—PORTION OF A TWIG OF *BUTEA FRONDOSA* ENCRUSTED BY *TACHARDIA LACCA* (actual size). INDIA.

The literature on the family is very extensive, and among the more comprehensive treatises on the structure and biology are Newstead's Monograph of the British species (1901–3), that of Green (1896–1922) on the Ceylon forms, and the writings of Berlese (1893–95), Marchal (1908), Lindinger (1912), Leonardi (1920) and Balachowsky (1932). A great deal of information on the anatomy of Coccids is given by Berlese (*l.c.*) and the student should also consult the papers of Mark (1877), Witlaczil (1886), Childs (1914), and Oguma (1919).

For nomenclature and a catalogue of the world species vide Fernald (1903).

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Order 15. NEUROPTERA (Alder Flies, Lacewings, Ant Lions, etc.)

SMALL TO RATHER LARGE SOFT-BODIED INSECTS WITH USUALLY ELONGATE ANTENNÆ. MOUTH-PARTS ADAPTED FOR BITING: LIGULA UNDIVIDED OR BILOBED OR OFTEN ATROPHIED. TWO PAIRS OF VERY SIMILAR MEMBRANOUS WINGS,[1] GENERALLY DISPOSED IN A ROOF-LIKE MANNER OVER THE ABDOMEN WHEN AT REST. VENATION PRIMITIVE BUT WITH MANY ACCESSORY VEINS: COSTAL VEINLETS NUMEROUS: Rs GENERALLY PECTINATELY BRANCHED. ABDOMEN WITHOUT CERCI. LARVÆ CARNIVOROUS, OF A MODIFIED CAMPODEIFORM TYPE WITH BITING OR SUCTORIAL MOUTH-PARTS: THE AQUATIC FORMS USUALLY WITH ABDOMINAL GILLS. PUPÆ EXARATE: WINGS WITH COMPLETE TRACHEATION.

The heterogenous group which formed the Neuroptera of Linnæus is now divided into at least eight or nine well-defined orders, the original name being confined to the Megaloptera and Planipennia as enumerated below. The group thus restricted is still further dismembered by some authorities into two or three separate orders. This course, however, is very doubtfully warranted owing to the difficulty of separating such orders on the basis of any constant venational differences. It is evident, however, that the Neuroptera exhibit at least three lines of evolution with marked divergence also in their metamorphoses. These several lines appear, however, to be derivable from a common ancestral type. The species are rarely abundant in individuals, and all exhibit weak powers of flight. They feed upon soft-bodied insects and liquid matter, such as honey-dew.

With the exception of the Coniopterygidæ, the Neuroptera are separable from the Mecoptera by the venational features enumerated above. The mouth-parts are well developed with biting mandibles, the maxillary palpi are 5-jointed, the labial palpi 3-jointed, and the ligula is reduced to the condition of a median and sometimes slightly bilobed process, or is totally atrophied. The wing-coupling apparatus is of the jugo-frenate type, though usually much reduced and without bristles: a frenulum, however, is present in many Hemerobiidæ. The tarsi are uniformly 5-jointed and the abdomen 10-segmented. Excepting for the venation (vide Tillyard, 1919), the comparative morphology of the order has been very inadequately investigated. There are two pairs of thoracic and eight pairs of abdominal spiracles, and the ventral nerve cord consists of three thoracic and generally seven abdominal ganglia. The digestive system is provided with a median dorsal food-reservoir, a peritrophic membrane is present, and the usual number of Malpighian tubes is eight: the ovaries consist of a variable number of usually polytrophic ovarioles.

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[1] The Coniopterygidæ are exceptional in having the two pairs of wings very unequal in size with greatly reduced venation. They are small insects covered with a whitish powdery exudation. The Nemopteridæ differ from all other families in their elongate, filiform hind wings.

The larvæ exhibit great diversity of structure and mode of life, but are, in all cases, carnivorous; in a considerable proportion of the species they are aquatic. The latter forms are interesting from the fact that they usually carry segmentally arranged, and often jointed, abdominal processes.

The Neuroptera are divided in the present work into the sub-orders Megaloptera and Planipennia, which are treated separately below. The British species number about 60, and for information concerning them see MacLachlan (1868) and Killington (1936–37). About 3,700 species of the order have been described.

Sub-order 1. MEGALOPTERA (Alder Flies and Snake Flies)

BRANCHES OF THE VEINS USUALLY WITHOUT A CONSPICUOUS TENDENCY TO BIFURCATE AT THE MARGINS OF THE WINGS. LARVÆ WITH BITING MOUTH-PARTS.

The Megaloptera fall very naturally into two superfamilies—the Sialioidea or "alder flies" and the Raphidioidea or "snake flies." These two divisions are regarded by Handlirsch as being sufficiently distinct to warrant their separation into orders of their own. They include a small number of archaic types not very closely related among themselves.

The sub-order is classified as follows:—

A (B).	—Prothorax quadrate: an exserted ovipositor wanting: wings without pterostigma. Larvæ aquatic.	**Sialioidea**
1.	Wing expanse 45–100 mm.: three ocelli present: 4th tarsal joint simple. Larvæ with 8 pairs of abdominal gills and no terminal filament.	CORYDALIDÆ
2.	Wing-expanse 20–40 mm.: ocelli absent: 4th tarsal joint bilobed. Larvæ with 7 pairs of abdominal gills and a terminal filament.	SIALIDÆ
B (A).	—Prothorax elongate: an exserted ovipositor present: wings with a pterostigma. Larvæ terrestrial.	**Raphidioidea**
3.	A single family.	RAPHIDIIDÆ

The **Sialioidea** are of special interest both on account of the large size and striking appearance assumed by certain of the species, and because the group includes the most generalized representatives of the Neuroptera. Similarly to other primitive groups, the Sialioidea only include a small number of genera and species, but they exhibit an almost world-wide although discontinuous distribution. They differ from other Neuroptera in the hind-wings being broad at their bases with the anal area folded fanwise when at rest (Fig. 382).

The eggs of these insects are laid upon leaves, stones and other objects, usually not far from water. They are deposited regularly in compact masses: in *Sialis* each mass contains 200 to 500 eggs and in *Corydalis* the number amounts to two or three thousand. The eggs are cylindrical with rounded ends and dark brown in colour: at its free extremity each is provided with a conspicuous micropylar apparatus varying somewhat in form among different genera. The young larvæ, after eclosion, make their way to the water: those of *Sialis* are found in the muddy bottoms of ponds, canals and slow-moving streams, while the larvæ of *Corydalis* lurk under stones in rapidly flowing water. All the larvæ of the Sialioidea are actively predaceous, devouring other insect larvæ, small worms, etc. The mouthparts resemble those of a Carabid larva, the mandibles being powerful and sharply toothed, while the maxillæ exhibit the typical parts and the labium consists of a mentum, a dentate ligula and 3-jointed palpi. The antennæ are prominent 4-jointed appendages, and the legs are well developed, terminating in paired claws. The larva of *Sialis* (Fig. 381) is provided with seven pairs of 5-jointed, lateral, segmentally arranged abdominal filaments or tracheal gills. Each of the latter is supplied by a tracheal branch and contains blood. On the 9th abdominal segment there is a terminal filament of a similar nature. In *Corydalis* and *Chauliodes* there are eight pairs of unjointed or imperfectly jointed filaments: in the former genus, and in *Neuromus*, each of the first seven abdominal segments also bears ventral, spongy tufts of accessory tracheal gills. The body in these three genera is terminated by a pair of hooked anal feet, without the gill-like filament of *Sialis*. According to Davis (1903), there are eight pairs of small abdominal spiracles in *Sialis*, while in *Corydalis* and *Chauliodes* thoracic spiracles are also present. Pupation occurs in the soil or in moss, etc., sometimes at a depth of several inches. The pupæ are exarate and are able to work their way to the surface to allow of the emergence of the imagines. In the common European *Sialis lutaria* the whole life-cycle occupies about a year. This species and *S. fusconebulosa* are the only British members of the super-family. *Corydalis* is North American and Asiatic and the male has enormously elongate sickle-like mandibles and a wing-expanse ranging up to 150 mm. For a general account of the biology of the Sialoidea vide Davis (1903). Some account of the anatomy of *Sialis* is given by Dufour (*Ann. Sci. Nat.* (3), 9, 1848), and by Loew (*Linn. Ent.* 3, 1848): the latter author also contributes observations on the anatomy of *Raphidia* (vide below).

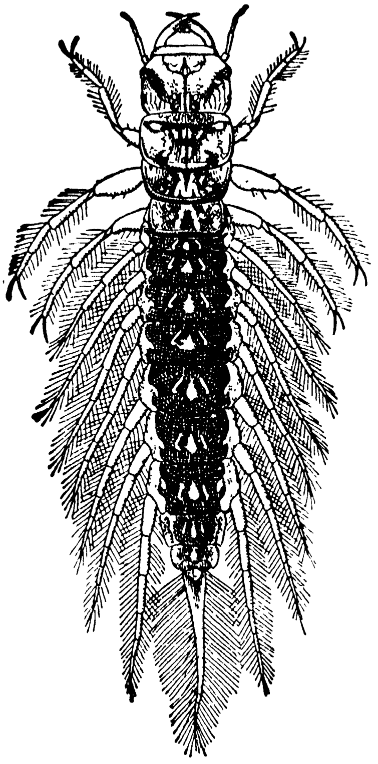

FIG. 381.—LARVA OF SIALIS LUTARIA. ENLARGED.
After Lestage.

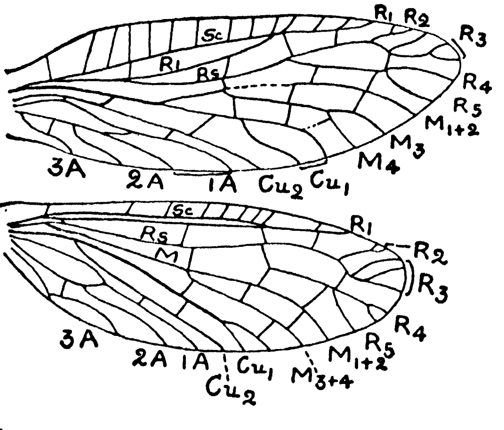

FIG. 382.—RIGHT WINGS OF *SIALIS LUTARIA*.

The **Raphidioidea** include the most specialized members of the Megaloptera and are entirely terrestrial in habits. The group occurs on all continents with the exception of Australia, and most of the species are included in the genera *Raphidia* (Fig. 383) and *Inocellia*. The imagines are remarkable for the elongated prothorax which, together with the narrowed posterior region of the head, forms a kind of "neck": unlike the Sialioidea, they possess an elongate setiform ovipositor. About eighty species of the group are known, of which four, belonging to the genus *Raphidia,* have been recorded from Britain. They occur in wooded regions and are met with among rank herbage, on flowers or tree-trunks, etc. The eggs are inserted by means of the long ovipositor in slits in the bark: they are elongate-cylindrical with a small appendage at one extremity. The larvæ occur under loose bark, particularly of conifers, and are very voracious, preying upon small soft-bodied insects which frequent similar situations. The larva of *Raphidia* (Fig. 384) is elongate and slender with a well chitinized head and prothorax. The thoracic legs are long, the abdomen carries no processes or appendages, and the mouth-parts resemble those of the imago. The pupa is more primitive than in any other of the Endopterygota and closely resembles the adult insect in its essential structural characters. Although first enclosed in a kind of cell the pupa emerges after a lapse of some time and, becoming active, crawls about until it finds a suitable place, where it remains until the eclosion of the imago.

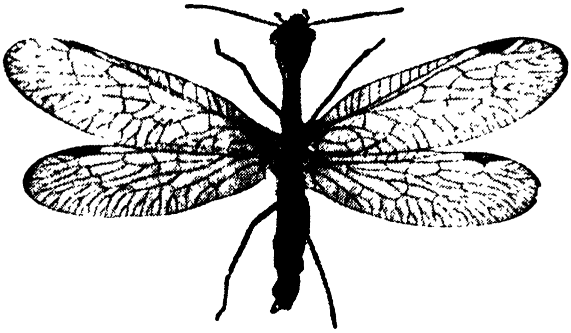

FIG. 383.—*RAPHIDIA NOTATA*, BRITAIN × 2½.

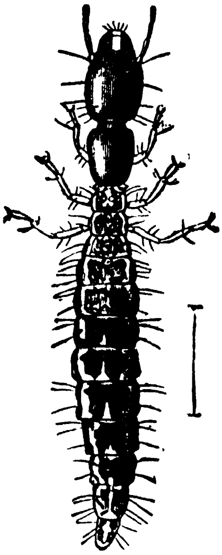

FIG. 384.—*RAPHIDIA NOTATA*, LARVA.

After Sharp, *Camb. Nat. Hist.*

The Raphidioidea have been monographed by Esben-Petersen (1913) and by Navas (1918).

Sub-order II. **PLANIPENNIA** (Lacewings, Ant Lions, etc.)

BRANCHES OF THE VEINS USUALLY CONSPICUOUSLY BIFURCATED AT THE MARGINS OF THE WINGS. LARVÆ WITH SUCTORIAL MOUTH-PARTS.

The Planipennia include the majority of the Neuroptera and their various families exhibit an exceptional wealth of venational specialization. Different as many of the families are in their imaginal characters, the group is well defined as a whole owing to the universal occurrence of suctorial piercing mouth-parts in the larvæ. Nearly all the Planipennia are terrestrial insects, a small number are more or less amphibious in their larval stages, and one or two genera have truly aquatic larvæ. The most generalized family are the Ithonidæ, which, to some extent, serve as a connecting link between the two sub-orders of Neuroptera.

The larvæ of the Planipennia are universally predaceous and are of considerable importance as destroyers of aphides and other injurious insects. The head is often large and very freely articulated with the prothorax. The mandibles and maxillæ are long and exserted, being thereby adapted for seizing the prey (vide Meinert, 1889). The first-mentioned appendages are usually sickle-shaped and, in some families, armed with teeth. They are grooved along their ventral surfaces, and the maxillæ, which closely resemble them in size and shape, fit one into each groove: in this manner the two sets of appendages form a pair of imperfect suctorial tubes. The combined organs are deeply inserted into the prey and its juices are imbibed by means of the pumping action of the pharynx. At the base of each maxilla there is usually a pair of small sclerites—the cardo and stipes—but, as a rule, maxillary palpi are absent. The labium is greatly reduced, and its palpi, although sometimes aborted, are very variable in different families. The antennæ are filiform and often rather long. The prothorax is divided into three more or less distinct sub-segments, but the meso- and meta-thorax are sometimes merged into the trunk and not sharply demarcated. The legs are long and slender and allow of activity of movement; their tarsi are single-jointed. The abdomen consists of ten segments and is devoid of cerci. The larvæ usually pass through three instars, except in *Ithone* where there are five: when about to pupate, they construct oval or spherical cocoons either of silk or of foreign particles bound together with that material. The pupæ possess strong mandibles which are utilized in cutting through the cocoons to allow of the emergence of the imagines. The diet of the larvæ consists solely of animal juices, and there is no through passage from the mid-intestine to the anus. The Malpighian tubes are usually 8 in number and, of these, 6 have acquired a secondary attachment by their distal extremities to the wall of the hind-intestine. The tubes thus modified function as silk-producing organs in the last instar, the silken thread being emitted by means of an anal spinneret (vide Anthony, 1902). The respiratory system opens by nine pairs of spiracles, the 1st pair being prothoracic and the remainder abdominal in position.

The Planipennia may be classified according to the following key: only five of the undermentioned families (marked*) are represented in the British fauna, and a useful account of their structure and biology has recently been contributed by Withycombe (1922).

1 (2).—Venation greatly reduced: small species covered by whitish powdery exudation. *CONIOPTERYGIDÆ (p. 404)
2 (1).—Veins and cross-veins numerous.
3 (4).—Fore-legs raptorial. MANTISPIDÆ (p. 404)
4 (3).—Fore-legs not raptorial.
5 (6).—Hind-wings greatly elongated and ribbon-like. NEMOPTERIDÆ (p. 402)
6 (5).—Hind-wings not as above.
7 (10).—Antennæ thickened distally or clavate.
8 (9).—Antennæ not half as long as fore-wing: wings with a very elongate hypostigmal cell extending beyond the fusion of Sc with R_1. MYRMELEONIDÆ (p. 403)
9 (8).—Antennæ more than half as long as fore-wing: an elongate hypostigmal cell wanting. ASCALAPHIDÆ (p. 404)
10 (7).—Antennæ not thickened distally.
11 (16).—Two or more branches of Rs in fore-wing arising from the apparently fused stems of R_1 and Rs.
12 (13).—Antennæ moniliform: cross-veins few. *HEMEROBIIDÆ
13 (12).—Antennæ not moniliform: cross-veins more numerous. (p. 398)
14 (15).—Hemerobiid-like: antennæ of male coarsely pectinate: ovipositor exserted. DILARIDÆ (p. 398)
15 (14).—Moth-like: antennæ filiform in both sexes: ovipositor not exserted. ITHONIDÆ[1] (p. 398)

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[1] In the genus *Ithone*, Rs is as in (16) but the moth-like appearance of these insects renders them easily recognisable.

16 (11).—All the branches of Rs arising from the latter vein after it has diverged from R.
17 (20).—Sc not joined at its apex with R_1.
18 (19).—Body and wings not hairy. *CHRYSOPIDÆ (p. 400)
19 (18).—Body and wings densely hairy. BEROTHIDÆ: part (p. 400)
20 (17).—Sc joined at its apex with R_1.
21 (22).—Wings rounded with a prominent " mid-rib " formed by Sc, R_1 and Rs. PSYCHOPSIDÆ (p. 400)
22 (21).—Wings more elongate and without any prominent " mid-rib " as above.
23 (24).—Cross-veins numerous. *OSMYLIDÆ (p. 399)
24 (23).—Cross-veins few.
25 (26).—Costal veinlets branched in fore-wing: scales present on some part of the wings in the female. BEROTHIDÆ: part (p. 400)
26 (25).—Costal veinlets unbranched in fore-wing: wing-scales absent. *SISYRIDÆ (p. 399)

In addition to the above families there are several others of minor importance. The *Sympherobiidæ* comprise several genera related to the Hemerobiidæ but differing in the formation of Rs. *Psectra* has the hind-wings of the male reduced to small scales: *P. diptera* is an extremely rare insect which has occurred once or twice in the British Isles. The *Myiodactylidæ* appear to be a sub-family of the Osmylidæ, and the *Nymphidæ* are a small family of Australian insects which are to be regarded as the remains of an ancestral group from which the Myrmeleonidæ have arisen. They have rather long filiform antennæ, which are moderately thickened, and differ from the last-mentioned family in the presence of cross-veins between Sc and R_1. The common N. American lacewing *Polystoechotes* belongs to the small family *Polystoechotidæ*, which is closely related to the Berothidæ.

FAM. ITHONIDÆ.—This family is the most nearly related to the Megaloptera of all the Planipennia. Its members are large and rather stout-bodied insects, of superficially moth-like appearance, with a wing-expanse of about 40 to 70 mm. Three genera and about half a dozen species are known: they frequent sandy localities in Australia and Tasmania (vide Tillyard, 1919, VIII: 1922). Ithonidæ are active runners taking refuge in dark crevices, etc., and when their wings are closed they bear a certain superficial resemblance to cockroaches. The eggs of *Ithone* are laid in sand which adheres to them owing to a sticky secretion with which they are covered: the larva is soft, whitish, and blind, of melolonthoid form, with small mandibles and maxillæ: it normally preys upon scarabæid larvæ.

FAM. DILARIDÆ.—A very small family recognizable from its allies by the strongly pectinated antennæ of the male and the exserted ovipositor of the female. Its affinities lie with the Hemerobiidæ and Ithonidæ, but nothing is known concerning its biology. *Dilar* occurs in N. America and Japan.

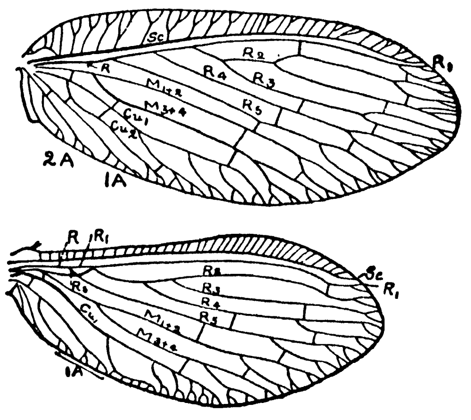

FIG. 385.—RIGHT WINGS OF *HEMEROBIUS*.

FAM. HEMEROBIIDÆ (Brown Lacewings).—This family was originally held to include all neuropterous insects whose larvæ possess suctorial mouth-parts and whose imagines have a closely reticulated wing-venation. The growth of further knowledge, and more particularly the work of Handlirsch and of Tillyard, have made it evident that the group thus constituted really forms a complex of a number of separate families. The Hemerobiidæ, as now restricted, are rather small delicate insects with moniliform antennæ and no ocelli. Their principal venational feature is the fusion of R_1 and Rs, two or more of the branches of the latter vein arising from the common stem thus formed. The costal area is crossed by numerous branched veinlets, true cross-veins are few and of a specialized character (Fig. 385). A further character is afforded by

Sc, which does not unite at its apex with any other vein. A wing-coupling apparatus of the jugo-frenate type is commonly present, and, although the jugal bristles are wanting, those of the frenulum are evident. The eggs, unlike those of the Chrysopidæ, are devoid of pedicels and have a knob-like micropylar apparatus. Hemerobiid larvæ (Fig. 386) are fusiform and smooth without tubercles of any kind, and the body hairs are simple. The mouth-parts are rather stout and only slightly curved. A reduced pad-like empodium is present between the tarsal claws, but in the first instar it is trumpet-shaped. In colour the larvæ are commonly creamy white with markings of some shade of brown. They roam about vegetation infested with aphids and other Homoptera, acari, etc., which serve as their food. As a rule these larvæ are naked, and the often repeated statement that they are concealed by skins of their victims which they transfer, along with other debris, to their backs, needs confirmation, and in most cases probably refers to Chrysopids. Hemerobiidæ are a widely distributed family, and rather more than 20 species occur in the British Isles.

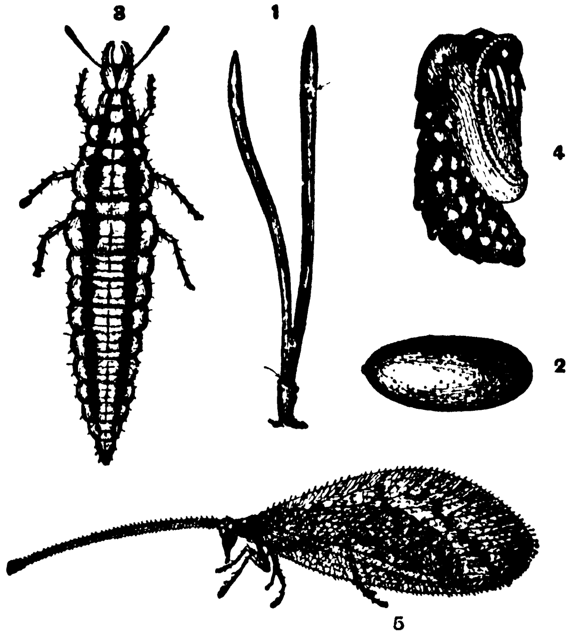

FIG. 386.—*HEMEROBIUS STIGMA.*

1. leaves of pine, the arrows indicate positions where eggs are laid, 2, egg × 30; 3, larva × 6; 4, pupa × 6; 5, imago × 4. *After* Withycombe, *Entom.* 1922.

FAM. OSMYLIDÆ.—This family is closely allied to the Sisyridæ and Berothidæ and is separable from the Chrysopidæ by the distal union of Sc and R_1, and by the presence of three ocelli near the frons. The very large number of cross-veins is also a characteristic of the family. The Osmylidæ are a considerable assemblage of beautiful insects, often with maculated wings, and *Osmylus chrysops* L. is the largest British Neuropteron. This species occurs locally along the borders of clear streams where there is a dense growth of bushes, etc. Its larva (Fig. 387) lurks under stones or about moss, etc., either in or near the water. It is easily recognized by its long slender stylet-like mandibles and maxillæ, which are only slightly curved upwards. Unlike the aquatic larva of *Sisyra* there are no gills and it breathes by means of thoracic and abdominal spiracles. According to Withycombe its natural food consists of dipterous larvæ.

FAM. SISYRIDÆ.—These insects are to be regarded as an offshoot of the Osmylidæ with which they agree in the distal fusion of Sc and R_1 and in the characters of Rs. On the other hand, the cross-veins are reduced in number and definitely specialized: the costal area, also, has no recurrent veinlet or branched transverse veinlets (Fig. 388). The larvæ of *Sisyra* and *Climacia* are aquatic, living in association with fresh-water sponges (*Spongilla* and *Ephydatia*). The life-history of *Sisyra* has been followed by Anthony (1902) and by Withycombe. The eggs are very small, resembling those of *Hemerobius*: they are laid in small clusters on leaves, piles, and other objects standing in or overhanging water. The female covers each batch with a silken web as in the Psocida. The larva clings to the surface of the sponge or descends into the open osteoles, piercing the sponge-tissue with its mouth-parts. It is yellowish green or brownish, hairy, resembling

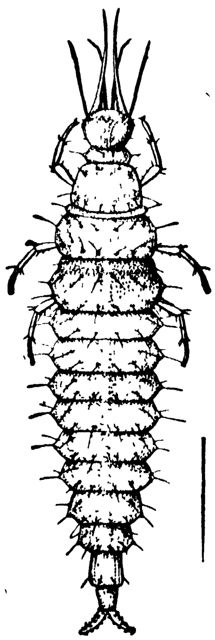

FIG. 387. — *OSMYLUS CHRYSOPS*, LARVA.

After Withycombe, *Trans. Ent. Soc.* 1922.

that of a Chrysopid in general form (Fig. 389); it bears seven pairs of segmentally arranged, several-jointed abdominal gills, each supplied by tracheal branches. The antennæ are long and setiform, while the mandibles and maxillæ form a pair of almost equally elongate bristle-like stylets. Labial palpi are wanting and the legs are single-clawed. Pupation takes place above water in a finely woven double cocoon. Three species of the genus occur in Britain, *S. fuscata* being common.

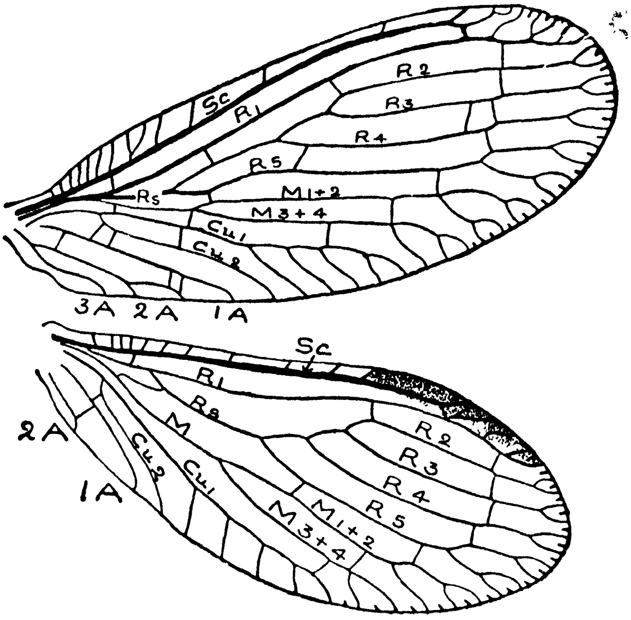

FIG. 388.—RIGHT WINGS OF *SISYRA FLAVICORNIS*. *After* Comstock, *Wings of Insects*.

FAM. BEROTHIDÆ.—The Berothidæ are rather small, somewhat slenderly built insects with variably shaped wings. The latter are hairy, especially along their posterior margins, and peculiar scales of a seed-like form may be present in the females, either on the posterior fringe or on some of the principal veins. The limits of the family, however, are ill defined: thus in some species Sc is distally joined with R_1, while in *Berotha* there appears to be no such union owing to the distal atrophy of Sc. These two veins remain separate in the Australian genera *Trichoma* and *Stenobiella*, which are narrow-winged, densely hairy insects: they are regarded by Tillyard (1916: IV) as constituting a family of their own—the Trichomatidæ. The eggs of *Spermophorella* are very similar to those of *Chrysopa* and are elevated upon long pedicels. The newly hatched larva is figured by Tillyard: it has an elongate narrow head with straight and rather short mandibles with broadened bases. The family is widely distributed and known from India, the United States and Australia.

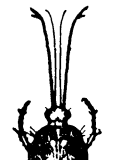

FIG. 389.—*SISYRA FUSCATA*, LARVA.

After Withycombe, *Trans. Ent. Soc.* 1922.

FAM. PSYCHOPSIDÆ.—Although usually regarded as a component part of the Hemerobiidæ, this family is separable therefrom by its markedly different venational characters and the shortened antennæ. The costal area of the wings is exceptionally deep and the three veins Sc, R_1 and Rs exhibit increased chitinization and assume a parallel course as far as their terminal anastomosis (Fig. 390): they form, in this manner, a kind of broad mid-rib which renders these insects easily recognizable. The biology of the Australian *Psychopsis elegans* has been followed by Tillyard (1919, VII) and the life-cycle occupies about a year. The eggs are laid in January or February upon the bark of trees, especially Eucalypti: they are oval and each is provided with a small micropylar projection. The larva is characterized by the great size of the mandibles, which are sickle-like and devoid of teeth: the head is also large and its broad base is closely connected with the prothorax without any visible "neck." In their habits these larvæ are arboreal, living beneath bark: they probably only emerge from their hiding-places to seize the insects which come to feed upon the gum which exudes from the trees. There are three larval instars: about November they construct silken cocoons in crevices of the bark and the pupal stage lasts about three weeks. Psychopsidæ are rare insects of nocturnal habits: they occur in Australia, S. Africa, Tibet, China and Burma.

FAM. CHRYSOPIDÆ (Green Lacewings).—This family includes a large number of closely related species popularly known as "green lacewings" or "golden eyes." Many have bright green bodies and appendages, with the wing-veins similarly coloured,

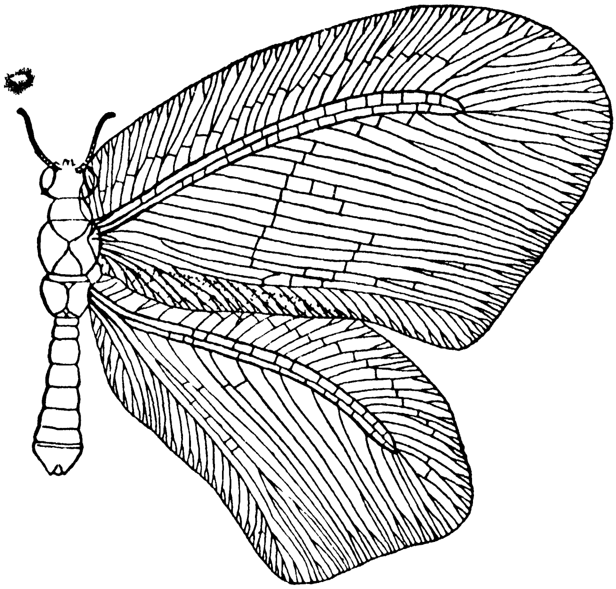

FIG. 390.—*PSYCHOPSIS GRACILIS*, MALE × 3.
Adapted from Tillyard, *Proc. Linn. Soc. N.S.W.* 43.

and the eyes exhibit a burnished metallic lustre. Certain of the species emit a disagreeable odour when handled from a pair of prothoracic glands, and have earned for the group the alternative name of "stink flies." The antennæ of the Chrysopidæ are filiform, and longer than they are in the preceding family, the joints being less distinctly demarcated. The venation (vide Tillyard, 1916, III) is characterized by Rs arising from the main stem separately from R_1, by the absence of a distal fusion between the latter vein and Sc, and by the exceptionally straight vein M. The latter and Cu are, however, highly complex veins, and for this reason they are designated by Tillyard pseudo-media and pseudo-cubitus respectively. The composition of these veins is represented in Fig. 391, and it will be noted that the pseudo-media is formed by the fusion of M_{1+2} and M_{3+4} and portions of the four proximal branches of Rs. The pseudo-cubitus is formed by Cu, by the distal portions of M_{1+2} and M_{3+4} and by parts of the three proximal branches of Rs.

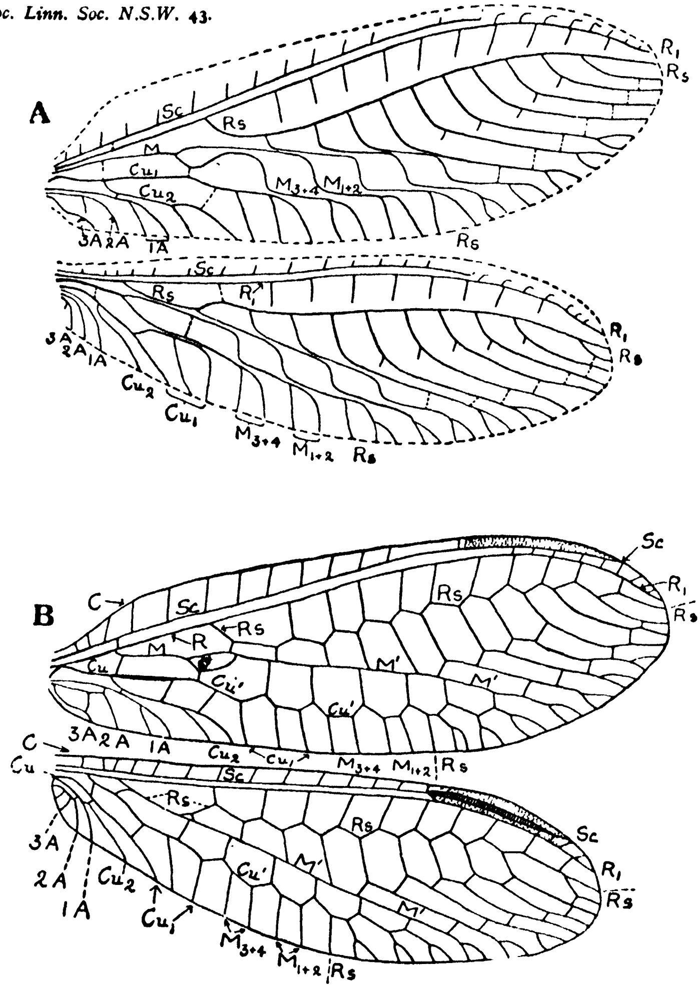

FIG. 391.—*CHRYSOPA SIGNATA.* A, DIAGRAM OF WING-TRACHEATION. B, WING-VENATION.
Cu^1, pseudo-cubitus; M^1, pseudo-media. *After* Tillyard, *Proc. Linn. Soc. N.S.W* 41.

The eggs of the Chrysopidæ are commonly laid in batches, and a small amount of secretory fluid accompanies each act of oviposition. A spot of this substance is applied to a leaf or other object and the abdomen is then uplifted, with the result that a viscous thread of the secretion is drawn out perpendicularly to the substratum. The thread rapidly hardens and is surmounted by an egg, the latter being thus supported upon a delicate pedicel. In *Chrysopa flava*, and certain other species, the pedicels of an egg-group are joined into a common bundle. Chrysopid larvæ (Fig.

392) resemble those of the Hemerobiidæ in their general characters but differ according to Withycombe in the following points. They are shorter and broader with the jaws more slender and curved. The body is provided with setæ arising from dorso-lateral tubercles. The larvæ are often concealed by the remains of their victims, which are retained in position by means of hooked hairs situated on the dorsal aspect of the abdomen. A trumpet-shaped empodium is present between the tarsal claws in all instars. *Chrysopa flava* differs from most other members of the family in its larva having no tubercles and in being more elongate. In coloration the larvæ are exceedingly variable: the ground colour is generally white, yellowish or green, usually with darker markings of red, chocolate or black. They are familiar objects on aphid-infested vegetation and are commonly obscured by their coating of debris. Economically, they are of importance on account of the large numbers of soft-bodied insects which they consume: their prey consists principally of aphides, but jassids, psyllids, coccids, together with thrips and acari, are also attacked. According to Wildermuth (*Journ. Agric. Res.* 6, 1916) *Chrysopa californica* will destroy 300–400 aphides during its larval existence. Rather more than a dozen species of the family are British, and 59 are enumerated by Navas in his monograph of the European forms (*Arx. Inst. Cien. Barcelona*, 1915).

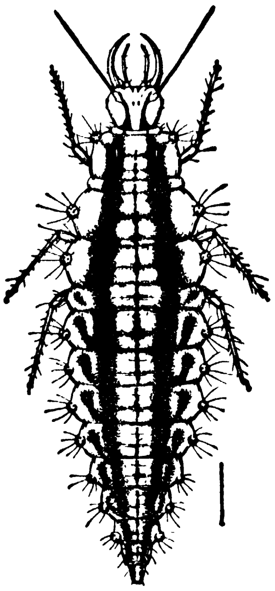

FIG. 392.—*CHRYSOPA VULGARIS*, LARVA IN 3RD INSTAR.

After Withycombe, *Trans. Entom Soc.* 1922.

FAM. NEMOPTERIDÆ.—A highly specialized family with enormously elongate, ribbon-like hind-wings and with the head usually prolonged into a kind of rostrum. They are striking and beautiful insects flying with a curious up-and-down motion after the manner of Ephemerids, with the long hind-wings streaming in the air. The form of the latter is somewhat variable: in *Croce* they are filiform, and taper to a point, while in other cases they are sometimes expanded before their extremities (Fig. 393). The mid-rib, which lends support to these greatly attenuated organs, is formed, according to Comstock, by the closely approximated stems of R and M. The life-history of the Indian *Croce filipennis* (Fig. 394) occupies about a year (vide Imms, 1911). The imagines are crepuscular and frequent buildings. The eggs are laid among dust and refuse on floors, and the fully-grown larva has a large quadrate head and long, curved, finely dentated mandibles. The head is connected with the hind-body by a conspicuous 2-segmented "neck"; the meso- and meta-thorax are imperfectly differentiated and merged into the abdomen. The larvæ cover themselves with dust particles and are hard to detect: they prey upon Psocids and

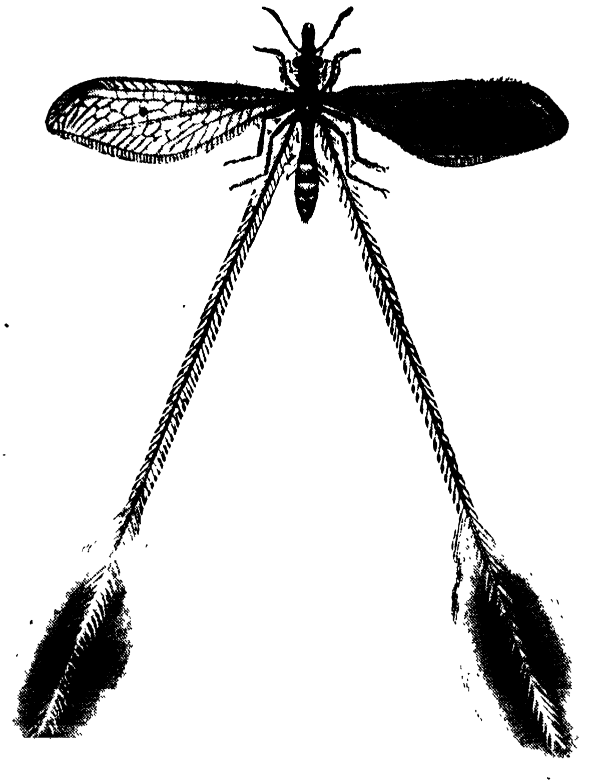

FIG. 393.—*CROCE FILIPENNIS* × 2·5. INDIA.

other small insects. The pupa is notable on account of its method of accommodating the long hind-wings. These are many times coiled after the manner of watch-springs: they cross each other near their bases, so that the right wing lies on the left side and *vice versa*. The pupa is enclosed in a cocoon composed of sand and debris bound together by silk. In *Nina joppana* and *Pterocroce storeyi* the neck of the larva is so greatly attenuated that it equals in length the whole of the rest of the body (Fig. 395): these remarkable larvæ have been bound in caves in Egypt and Palestine (vide Withycombe, 1923). The family is widely distributed and several species occur in S. Europe.

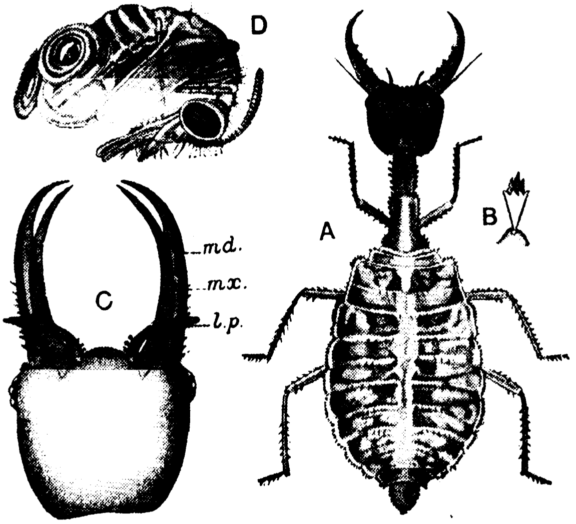

FIG. 394.—*CROCE FILIPENNIS*.

A, larva in last instar. B, a dolichaster × 230. C, ventral aspect of head of larva × 50; *md*, mandible; *mx*, maxilla; *lp*, labial palp. D, pupa. *After* Imms, *Trans. Linn. Soc.* 1911.

FAM. MYRMELEONIDÆ (Ant Lion Flies). — In their general appearance these insects resemble dragonflies of the narrow-bodied type and in their larval stages they are known as "ant lions" (fourmilions). They comprise a considerable number of often large, handsome species which, however, are seldom seen. During the day they hide among trees and bushes, only appearing on the wing towards dark. Myrmeleonidæ are easily distinguished from other Neuroptera by their short knobbed antennæ: their wings are long and narrow, usually marked with brown or black, and furnished with many accessory veins and cross-veins. They are closely related to the Ascalaphidæ, but the latter insects have longer antennæ and lack the elongate hypostigmal cell (Fig. 396). Although most abundant in tropical countries, species of *Myrmeleon* occur in Europe, one representative being found as far north as southern Sweden, but the family is not found in the British Isles: the European species are enumerated by Navas (*Insecta*, 5, 1915). The biology of *M. formicarius* was accurately observed by the early naturalist Reaumur. The ova are deposited in sand and the newly emerged larvæ excavate pits in the ground for the purpose of securing their prey. The Myrmeleonid larva buries itself at the bottom of the pit, leaving only its large jaws protruding. An ant or other insect wandering over the edge of the pit usually dislodges the sand of the sloping sides and soon finds itself in difficulties. The ant lion jerks some of the sand by means of its head towards its victim and continues to do so until the latter is brought to the bottom of the pit. Here it is seized and not released until its juices are extracted. The larvæ of this family (vide Meinert, 1889; Redtenbacher, 1884; Gravely and Maulik, 1911) are flattened and ovoid with large heads, and long, protruding mandibles, armed with exceedingly sharp spiniform teeth (Fig. 397). The pit-forming habit is characteristic of *Myrmeleon* and several other genera, but the larva

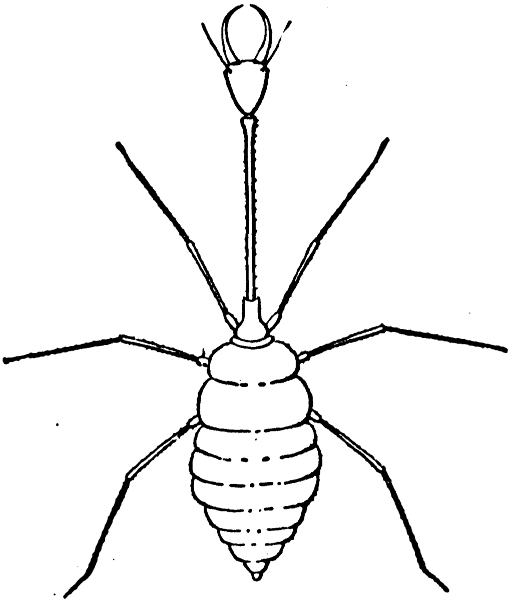

FIG. 395.—*PTEROCROCE STOREYI*, LARVA IN LAST INSTAR × circa 8.

After Withycombe.

of *M. contractus* lives on the mud-covered trunks of trees in Bengal, and doubtless preys upon the ants which are constantly streaming up and down. Other larvæ of this family hide away under stones and debris, or cover themselves with a coating of foreign substances, and thereby secure concealment. Some account of the anatomy of the imago is given by Dufour (*Ann. Sci. etrang.* 7, 1834).

FAM. ASCALAPHIDÆ.—This family is closely related to the Myrmeleonidæ and has a very similar distribution. Some of the species are active fliers, and are on the wing during daytime, hawking their prey after the manner of dragonflies: others, however, are nocturnal and very seldom seen. The eggs are deposited in rows upon grass stems, twigs, etc., and the batches are often fenced in below by circles of rod-like bodies or repagula which possibly guard them from the attacks of predaceous enemies. The larvæ closely resemble those of the preceding family and have similar dentate mandibles: they are often provided with lateral segmental processes fringed with modified setæ (dolichasters). These processes are particularly well developed in *Pseudoptynx* and *Ulula*, while they are usually quite rudimentary in the Myrmeleonidæ. The larvæ do not construct pitfalls but live concealed on the ground among stones, leaves, etc., or more rarely on the bark of trees. The family has been monographed by Van der Weele (1908), who figures larvæ of several genera: the life-history of *Ascalaphus* is discussed by Westwood (*Trans. Ent. Soc.* 1888) and that of *Ulula* by McClendon (*Amer. Nat.* 36, 1902). Several species are common in southern Europe and *Ascalaphus longicornis* occurs as far north as Paris.

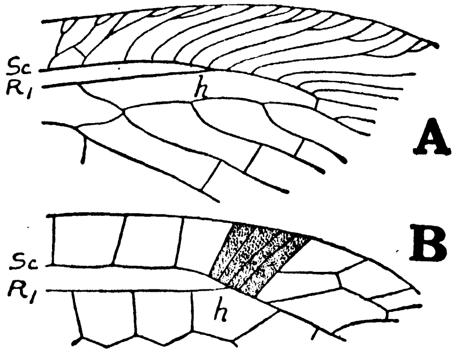

Fig. 396.—Portion of Fore-wing of A, A Mymeleonid; B, An Ascalaphid, showing Hypostigmal Cell *h*.

Based on figures by Comstock.

FAM. MANTISPIDÆ.—The members of this family are easily recognized by the elongate prothorax and the large raptorial anterior legs. The latter appendages are formed very much the same as in the Mantidæ (vide p. 244) and fulfil similar functions. Each femur is armed with powerful spines and the tibia is adapted to fold closely on to it, the two joints forming a very effective prehensile organ for seizing the prey. The family occurs in most of the warm regions of the world and a few species occur in S. Europe. The life-history of *Mantispa styriaca* has been followed by Brauer (*Verh. zoo. bot. Ges. Wien*, 19, 1869). The eggs are borne on long pedicels as in *Chrysopa* and the newly-hatched larvæ are elongate and campodeiform but are devoid of cerci. They pass into hibernation almost immediately and in the following spring they seek out the egg-cocoons of the spider *Lycosa*. Only a single *Mantispa* larva enters each cocoon and it preys upon the young spiders, piercing them with the pointed mouth-parts and imbibing their body-fluids. Feeding in this manner leads to an expansion of the larva which becomes so swollen as to resemble that of a miniature cockchafer. It subsequently undergoes ecdysis, and becomes transformed into an eruciform larva with a minute head, and small thoracic legs. It becomes mature a few days later, and spins a cocoon around itself, amidst the dried remains of its victims, within the original egg-bag of the spider. Pupation occurs within the last larval skin and the imago consequently has to pierce the latter and its own cocoon, and that of the spider, before it emerges into the open. The parent spider watches over her cocoon without hostility to the presence of the parasite. The life-history of *Mantispa*, it will be observed, affords an example of hypermetamorphosis.

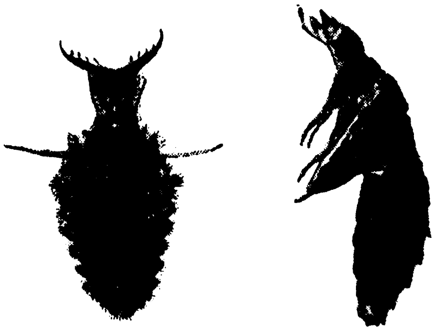

Fig. 397. — *Myrmeleon*, Larva and Pupa × 3. Switzerland.

From enlarged photos by H. Main.

FAM. CONIOPTERYGIDÆ.—This family includes about 50 species which are the smallest and most aberrant of the Neuroptera. They are extremely fragile insects bearing a general resemblance to aphides, with the body and wings covered with a whitish powdery exudation. The antennæ are filiform and the joints vary between about 16 and 43 in number: the eyes are rather large and there are no ocelli. The mouth-parts do not differ in any important features from those of other Planipennia. The venation is greatly simplified by reduction, Rs being 2-branched, and there are but few cross-veins (Fig. 398). Perhaps the strongest claims these insects have to be regarded as Neuropterous rests on the structural characters of their larvæ. So far as known the eggs are laid upon various trees frequented by Aphididæ, Coccidæ or Acarina, and the resulting larvæ prey upon those organisms. The larvæ are more or less pyriform, tapering sharply towards the hinder extremity, and the legs are long and slender (Fig. 399). The antennæ are few-jointed and fringed with rather long hairs: the mandibles and maxillæ are short and stout piercing organs, and the labial palpi are conspicuous clavate appendages projecting in front of the head. When about to pupate a cocoon is spun of silk emitted from the anus as in other Planipennia. According to Arrow (*Ent. Month. Mag.* 1917) the first generation of *Conwentzia psociformis* spins its cocoons on oak-leaves, while the second generation overwinters as larvæ, which lie up in cocoons spun upon the trunk of that tree. The family has been monographed by Enderlein (1906): although its members are not rare they need carefully looking for and, up to the present, only about seven species have been found in Britain (vide Withycombe, *Entom.* 1922). Anatomically the larvæ differ from other Planipennia in possessing only six Malpighian tubes and in the greatly concentrated abdominal nerve cord.

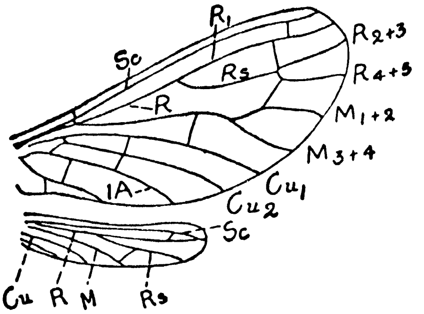

FIG. 398.—*CONWENTZIA PSOCIFORMIS*, RIGHT WINGS × 12.

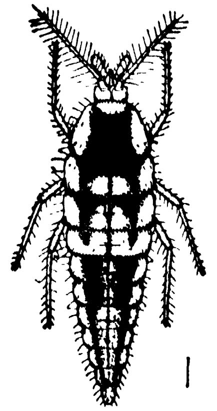

FIG. 399.—*CONWENTZIA PSOCIFORMIS*, LARVA. *After* Withycombe, *Trans. Ent. Soc.* 1922.

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Order 16. MECOPTERA (**Panorpatæ:** Scorpion flies)

SLENDER, MODERATE OR SMALL-SIZED, CARNIVOROUS INSECTS WITH ELONGATE, FILIFORM ANTENNÆ. HEAD USUALLY PRODUCED INTO A VERTICALLY DEFLECTED ROSTRUM, WITH BITING MOUTH-PARTS: LIGULA WANTING. LEGS LONG AND SLENDER. WINGS SIMILAR AND MEMBRANOUS, CARRIED LONGITUDINALLY AND HORIZONTALLY IN REPOSE: VENATION PRIMITIVE, Rs DICHOTOMOUSLY BRANCHED, Cu_1 SIMPLE. ABDOMEN ELONGATE WITH SHORT CERCI, MALE GENITALIA PROMINENT. LARVÆ ERUCIFORM WITH BITING MOUTH-PARTS AND THREE PAIRS OF THORACIC LEGS: ABDOMINAL FEET PRESENT OR ABSENT. PUPÆ EXARATE: WINGS WITH REDUCED TRACHEATION.

This small order comprises fewer than 300 species, the greater number of which belong to the genera *Panorpa* and *Bittacus*. The majority of the members of the group are easily recognized by the beak-like prolongation of the front of the head, and their often maculated wings. The "scorpion flies" (*sen. str.*) belong to the Panorpidæ, which include many species widely spread over the northern hemisphere (Fig. 400). Their vernacular name is due to the fact that the males carry the terminal segment of the abdomen upwardly curved, somewhat after the manner of Scorpions. The Bittacidæ are very slender Tipula-like insects with prehensile tarsi: they are found in most parts of the world excepting the northern portion of the holarctic region. The Boreidæ are characterized by their vestigial wings and occur in Europe and N. America. The order is represented in the British Isles by three species of *Panorpa* and a single species of *Boreus* (vide MacLachlan, 1868).

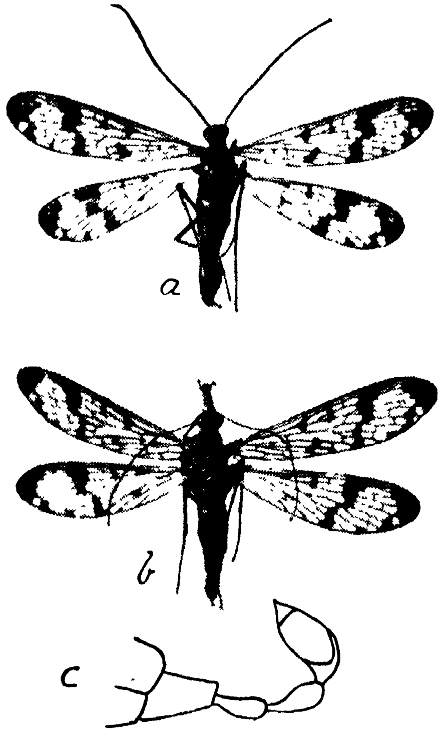

FIG. 400.—*PANORPA COMMUNIS.* A, MALE; B, FEMALE (from Photos *by* W. J. Lucas); C, APEX OF ABDOMEN OF MALE (*after* MacLachlan).

The Mecoptera are essentially terrestrial insects undergoing their transformations in the soil: a possible exception is found in *Nannochorista*, which is believed by Tillyard to be aquatic. Both their larvæ and imagines are carnivorous, but the extent to which the Panorpidæ prey upon living uninjured insects or other animals is doubtful. Brauer and Felt have reared larvæ of *Panorpa* upon fragments of meat, but Miyake found wounded or dead insects more acceptable. The adults are mostly found in shaded situations where there is a growth of rank herbage. *Bittacus* rests suspended from grasses or twigs by its fore-legs, and preys upon small Diptera, seizing them by means of its raptorial tarsi. *Boreus* lives among moss or beneath stones in autumn and early winter, appearing occasionally on the surface of snow; it is exceptional in feeding upon vegetable matter.

External Anatomy (Fig. 401).—The anterior region of the head is usually prolonged into a rostrum which is formed by the elongation of parts of the head-capsule together with the clypeus, labrum and maxillæ. The compound eyes are well developed and there are usually three ocelli. The antennæ are more or less filiform and many-jointed, there being about 40–50 joints in *Panorpa*, and about 16–20 in *Bittacus*. The mandibles are slender and elongate: they are only dentate at their apices, each bearing from 1 to 3 sharp teeth. The maxillæ are complete: their palpi are 5-jointed, and the galeæ and laciniæ are hairy lobes of somewhat complex structure (vide Miyake, 1913). The labium consists of an elongate submentum, not always clearly differentiated from the short mentum: the prementum exhibits traces of a bilobed structure, but the ligula has disappeared. The labial palpi are 1- to 3-jointed; in some cases they are in the form of fleshy lobes in which, according to Crampton, traces of pseudotracheæ may be present, resembling those found in the labium of Diptera. The mouth-parts of *Nannochorista* are considerably specialized (vide Tillyard, 1917). The labrum and epipharynx form a sharply projecting process, the mandibles are vestigial, and the labial palpi (paraglossæ of Tillyard) are partially fused at their bases. This genus, which is accorded separate family rank by Tillyard, exhibits a tendency towards the development of suctorial mouth-parts and foreshadows the condition found in the lower Diptera.

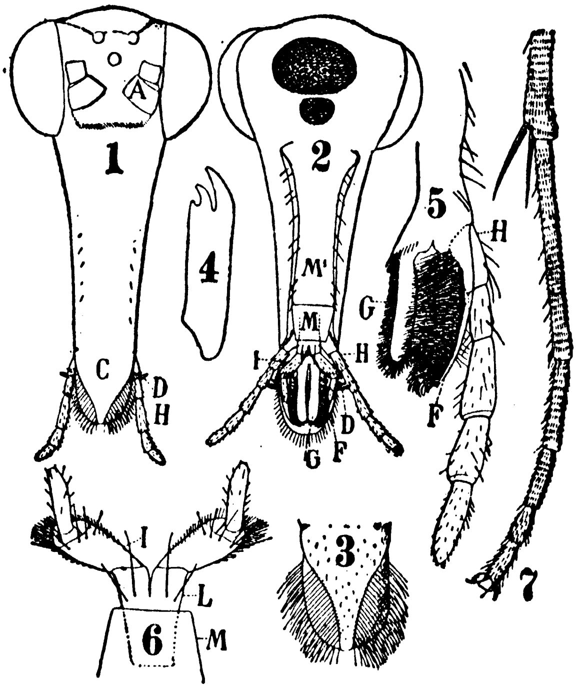

Fig. 401.—*Panorpa communis.* 1, Frontal view of Head; 2, Ventral view; 3, Labrum; 4 Mandible; 5, Maxilla; 6, Labium; 7, Apex of Tibia and Tarsus.

A, antenna; C, labrum; D, mandible; F, galea; FC, fronto-clypeus; G, lacinia; M, mentum; M¹, submentum. *After* Silvestri, with legend modified.

The prothorax is very small, its largest region being the notum, which is divided by transverse lines into four areas. Both the meso- and metathorax are well developed. The legs are generally adapted for walking, the claws are usually paired and in *Panorpa* they are strongly pectinated. In *Bittacus* the claws are single, and the fourth and fifth tarsal joints are provided with fine teeth along their inner margins: the fifth joint is capable of closing on to the fourth after the manner of the blade of a pocket-knife. The two pairs of wings are similar in form and nearly equal in size: in many species they are conspicuously spotted or banded. These organs are totally absent in the Californian *Apterobittacus*: in the males of the Boreidæ (Fig. 402) they are represented by two pairs of slender bristle-like vestiges, and in the females there is a single pair of scale-like lobes on the mesothorax. In the Nannochoristinæ and Choristinæ there is a definite wing-coupling apparatus with a well-developed frenulum (vide p. 35). Microtrichia are generally present, and macrotrichia occur on the veins and their branches, but not on the cross-veins: the latter type of setæ is also often present on the wing-membrane. The venation is extremely archaic, the principal veins and their primary branches (excepting those of Cu_1) frequently being present (Fig. 403). The wing tracheæ, on the other hand, are highly specialized by reduction. The primary dichotomies of the veins usually occur fairly close to the bases of the wings, and cross-veins are numerous, but without definite arrangement. In their venational features the two pairs of wings are also very alike, the principal difference being the basal fusion of Cu_2 and 1A in the hind-wing. A marked deviation from the primitive type is exhibited in *Nannochorista* in which R_{2+3} is unforked and $M + Cu_1$ are fused for about half their length.

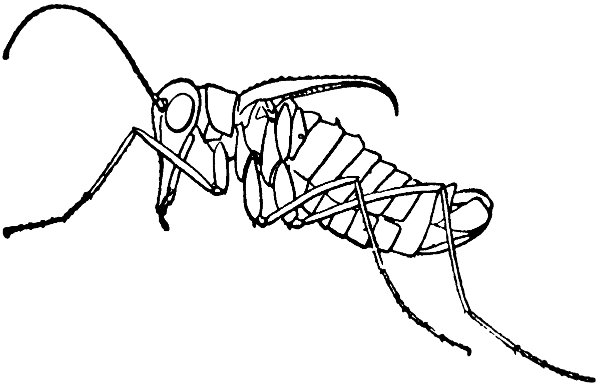

FIG. 402.—*Boreus hyemalis*, MALE × 15.
After Withycombe.

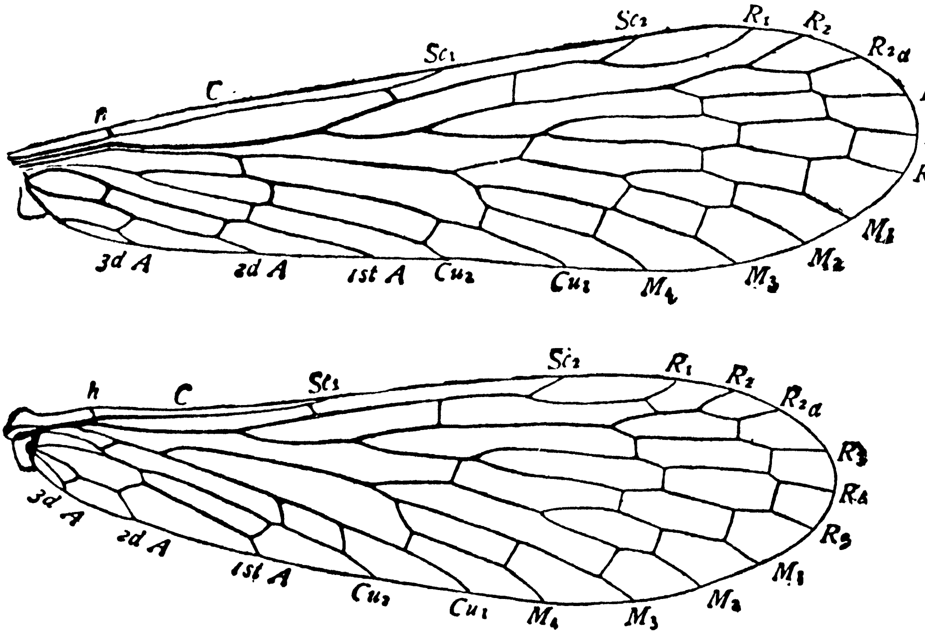

FIG. 403.—WINGS OF *PANORPA*.
After Comstock, *Wings of Insects*.

The abdomen is composed of 10 segments and, in the male of *Panorpa*, the hind margin of the 9th sternum is prolonged into a deeply cleft process, the two arms of which are styliform. The 9th tergum is prolonged into a subquadrate plate. Between the dorsal and ventral processes thus formed there is a pair of laterally inserted 2-jointed claspers. The 10th segment is very inconspicuous, and bears a pair of short 1-jointed cerci. Between the basal joints of the claspers is the longitudinally cleft ædeagus. In the female the 7th to 10th segments are cylindrical, and each is telescoped into the preceding segment: at the apex of the abdomen is a pair of 2-jointed cerci.

Internal Anatomy.—The internal anatomy (vide Miyake, 1913) has only been very partially investigated. In *Panorpa* the *alimentary canal* is a tolerably straight tube, the only convolution present occurring in the hind-intestine. The œsophagus is curiously dilated at two points along its course to form what appears to be a kind of muscular pumping-apparatus. A short distance further backward there is an elliptical chamber which is regarded as the proventriculus: the latter is provided with longitudinal and circular muscles, and its inner lining is beset with numerous long setæ. The mid-intestine is an elongate tube of large calibre, and the commencement of the hind-intestine is marked by the insertions of 6 Malpighian tubes. A pair of tubular salivary glands is also present. The *nervous system* consists of the usual cephalic centres, 3 thoracic and 6 abdominal ganglia: the first of the latter is located in the metathorax, and the remaining abdominal ganglia lie in the 3rd to 7th segments respectively. The *respiratory system* is well developed: there are two pairs of thoracic and six to eight pairs of abdominal spiracles. The *reproductive system* in the male consists of a pair of testes, each composed of three follicles arranged side by side around a longitudinal axis: the vasa efferentia are densely convoluted, forming a kind of epidydimis at the posterior end of the testis. The two vasa deferentia open separately into a large median vesicula seminalis which also receives a pair of accessory glands. Each ovary consists of 10–25 polytrophic ovarioles, the number varying according to the species. The two oviducts unite to form a common canal which opens into a kind of genital pouch: the latter also receives the opening of the duct leading from a small pyriform sac (spermatheca ?) and that of the duct of a pair of colleterial glands. The genital pouch communicates with the exterior on the 9th abdominal segment.

Life-history and Metamorphosis.—The eggs of several species have been obtained by confining the adults in vessels containing damp soil. In the European and American species of *Panorpa* they are laid in small batches in crevices in the soil: in the Japanese *P. klugi* Miyake mentions nearly 100 eggs being deposited in a group. In form they are ovoid in *Panorpa* and more or less cuboidal in *Bittacus*. The life-history of *Panorpa* was first observed by Brauer (1863); Felt (1895) describes the larva of *P. rufescens*, but the most complete account is that of Miyake (1912) which refers to *P. klugi* (Fig. 404). The first stage larva is yellowish-grey with the head testaceous. It is eruciform and bears a close resemblance to a caterpillar. The head is rather large with prominent 4-jointed antennæ and it bears a group of about 20–28 simple eyes on either side. The mandibles are sharply toothed, and the maxillæ are divided in lobes apparently corresponding with a galea and lacinia: the maxillary palpi are 4-jointed. The labium is small and its palpi 3-jointed. The thorax bears 3 pairs of legs, each composed of 4 joints: the abdomen is 10-segmented and the first 8 somites each carry a pair of abdominal feet. A median dorsal chitinized shield is present on all the body segments. The first 9 abdominal shields each carry a pair of annulated processes, the last two pairs being considerably the larger: the 10th segment bears a single median process of a similar character together with a curious retractile lobed vesicle on its ventral side. Nine pairs of spiracles are present: they are located on the prothorax and first 8 abdominal segments. After the first ecdysis the annulated processes practically disappear except those of the last three segments. The number of ecdyses that occur has not been observed: Felt, from head-measurements, recognized seven stages in *Panorpa rufescens*. Pupation takes place in an earthen cavity below ground: the pupa is of the usual exarate type and is capable of movement when disturbed: according to Miyake it works its way to the surface prior to the emergence of the imago. The European species probably pass through a single generation in the year. The larva of *Boreus* is strongly curved: the thoracic legs are well developed but there are no abdominal feet. It lives among moss and, when about to pupate, constructs a vertical tube leading near to the surface.

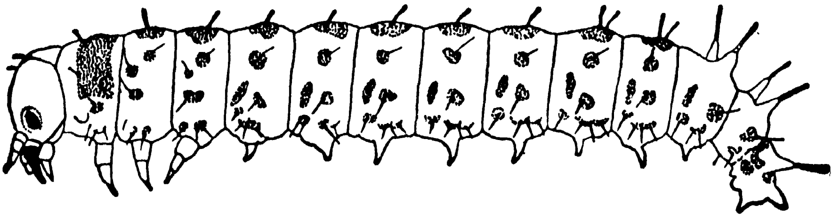

FIG. 404.—*PANORPA*, LARVA IN LAST INSTAR × 5.
Adapted from Miyake.

Classification.—The order has been recently monographed by Esben-Petersen (1921), whose family divisions are adopted below.

1 (2).—Tarsi single-clawed and modified for raptorial use. *Bittacus, Apterobittacus.* BITTACIDÆ
2 (1).—Tarsal claws paired and not modified for raptorial use.
3 (4).—Wings vestigial *Boreus.* BOREIDÆ
4 (3).—Wings well developed. *Panorpa, Chorista, Tæniochorista, Nannochorista.* PANORPIDÆ

In addition to the above, the two small families Notiothaumidæ and Meropidæ are represented each by a single genus and species from Chili and the United States respectively. They differ from the Panorpidæ in the shorter and broader wings which exhibit a more reticulated venation.

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Order 17. TRICHOPTERA (Phryganeidæ: Caddis Flies)

SMALL TO MODERATE-SIZED MOTH-LIKE INSECTS WITH SETACEOUS ANTENNÆ. MANDIBLES VESTIGIAL OR ABSENT: MAXILLÆ SINGLE-LOBED WITH ELONGATE PALPI: LABIUM WITH A MEDIAN GLOSSA AND WELL-DEVELOPED PALPI. WINGS MEMBRANOUS, MORE OR LESS DENSELY HAIRY AND HELD ROOF-LIKE OVER THE BACK IN REPOSE. FORE-WINGS ELONGATE HIND-WINGS BROADER WITH A FOLDING ANAL AREA: VENATION GENERALIZED CROSS-VEINS FEW. TARSI 5-JOINTED. LARVÆ AQUATIC, MORE OR LESS ERUCIFORM AND USUALLY LIVING IN CASES: BODY TERMINATED BY HOOKED CAUDAL APPENDAGES. PUPÆ EXARATE WITH STRONG MANDIBLES: WING TRACHEATION REDUCED.

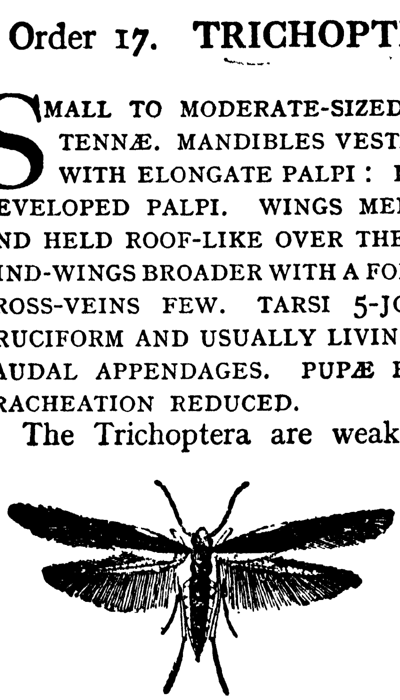

FIG. 405.—*Hydroptila angustella.* × 5.
After MacLachlan.

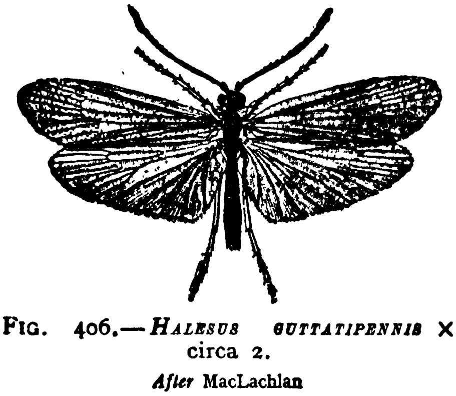

FIG. 406.—*Halesus guttatipennis* × circa 2.
After MacLachlan

The Trichoptera are weakly flying insects of moth-like appearance found in the vicinity of water (Figs 405, 406). They are unfamiliar to the general student, whose acquaintance with the order is usually restricted to the case-bearing larvæ which frequent ponds and streams. The imagines are mostly obscurely coloured, being generally some shade of brown, often with darker markings. They are not often seen on the wing unless disturbed, and they rest on herbage, trees, or stones their flight is of short and uncertain duration. Many species are nocturnal; some are attracted to a light, others to the moth-collector's saccharine mixture, and a few visit flowers. They have seldom been observed in the act of feeding: the mouth-parts are adapted for licking fluid nourishment, but probably a number of species take no food at all. In their general affinities they are very closely allied to the Lepidoptera-Homoneura and are only separable from the latter upon comparatively slight characters. In the Trichoptera, however, a thyridium is generally present on each wing, M_4 is separate from Cu_{1a} in the fore-wing and broad scales are universally wanting. About 2,600 species of the order are known and, of these, rather more than 170 inhabit the British Isles. The principal work on the European forms is that of MacLachlan (1870–80), who has also monographed the British species (1865). The best modern introduction to the order is by Ulmer (1909).

Anatomy (Fig. 407).—The antennæ are multi-articulate and setaceous, frequently several times the length of the wings: when in repose they are held closely porrected in front of the head. The compound eyes are usually small, but occasionally they occupy nearly the whole of the head in the male. Ocelli are either three in number or wanting. The structure of the mouthparts needs comparative study among representative genera. The clypeus is narrow and transverse, while the labrum is generally somewhat elongated. The mandibles are atrophied, or vestigial, in many genera such as *Phryganea, Limnophilus, Anabolia,* etc. (vide Lucas, 1893), but are better developed in certain others. The maxillæ are small and closely associated with the labium: they are ordinarily provided with a single lobe or mala, the palpi are elongated and 5-jointed in the females, but in the males the joints are more variable. The labium consists of a well-developed mentum, a median glossa, and 3-jointed palpi. There is a prominent hypopharynx which receives the aperture of the salivary glands. In the Australian *Plectrotarsus* the labrum and labium are greatly elongated, forming a kind of rostrum, and the two pairs of palpi are carried forwards. According to Cummings (1913) in *Dipseudopsis* each maxillary lobe is in the form of a pendulous, annulated half-tube recalling the condition found in certain archaic Lepidoptera in which the two elements of the proboscis are not co-adapted.

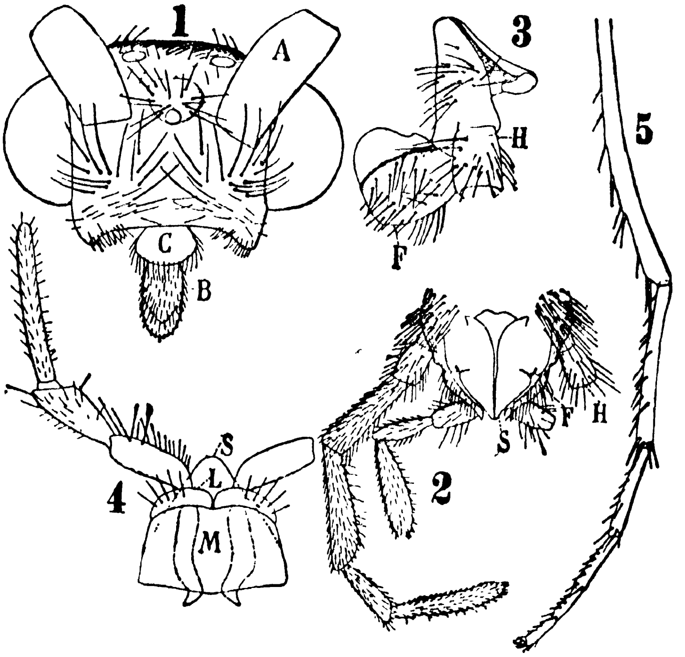

Fig. 407.—*Limnophilus.* 1, Head, frontal view. 2, Maxillæ and Labium (inner aspect). 3, Maxilla. 4 Labium. 5, Tarsus and Apex of Tibia of 3rd Leg.

A, base of antenna; B, labrum; C, clypeus; F, galea; H, base of maxillary palp; L, prementum; M, mentum; S, glossa. *After* Silvestri.

The prothorax is small and ring-like; the mesothorax is the largest segment and the metathorax is somewhat shorter. The legs are long and slender with large, strong coxæ: a meron is present in relation to the two hind pairs of coxæ, but is less completely developed than in most Lepidoptera. The tibiæ are often furnished with spines and movable spurs, the tarsi are 5-jointed, and between the claws there is either a pair of pulvilli or a cushion-like empodium. The wings are almost always fully developed, but the females of *Enoicyla* and *Philopotomus distinctus* are practically apterous. In *Anomalopteryx* (male) and *Thamastes* (both sexes) the hind-wings are reduced to scale-like rudiments. The extremely hairy nature of the wings, which is especially characteristic of the order, is due to the presence of macrotrichia both on the veins and wing-membrane. Certain genera, however, exhibit a tendency to a reduction of this clothing, and in some forms there is an almost general absence of hairs. Scattered scales of a primitive type are found on the wings of certain Trichoptera, but are narrow and acuminate, with few striæ, and do not assume the broadened form so characteristic of Lepidoptera. The fore-wings are denser than the hind-wings, and are often slightly more coriaceous. The wing-coupling apparatus is exhibited in a primitive condition in *Rhyacophila* in which there is a jugal lobe on the fore-wing resting on the costa of the hind-wing. There are neither jugal bristles nor frenulum, and the humeral lobe is suppressed or vestigial. In the majority of genera the jugal lobe is rudimentary or wanting, and an amplexiform type of coupling apparatus is developed. This is brought about by a fold along the whole length of the anal area of the fore-wing engaging the costa of the hind-wing. In some forms a row of costal hooks along the hind-wing grapple the anal margin of the fore-wing, and thus securely interlock the two wings of the side. The venation, as exemplified by *Rhyacophia fuscula*, is of an extremely generalized type (Fig. 408) and closely resembles that of the most primitive Lepidoptera. Almost all the veins are longitudinal, not more than two veinlets in the costal series are retained, and the cross-veins are reduced in number. Unlike the Lepidoptera, M$_4$ of the fore-wing is not fused with Cu$_{1a}$. Near the fork of vein M on both pairs of wings there is, ordinarily, a semi-transparent whitish spot generally devoid of hairs and known as the *thyridium*. It is possibly due to the presence of a gland or sensory organ and is wanting in Lepidoptera. The usual number of abdominal segments is 9. The genitalia in the male (vide Zander, 1901) consist of a pair of claspers and two lobes (parameres ?) of the aedeagus : in the female the terminal segments are sometimes retractile and tubular, thus functioning as an ovipositor.

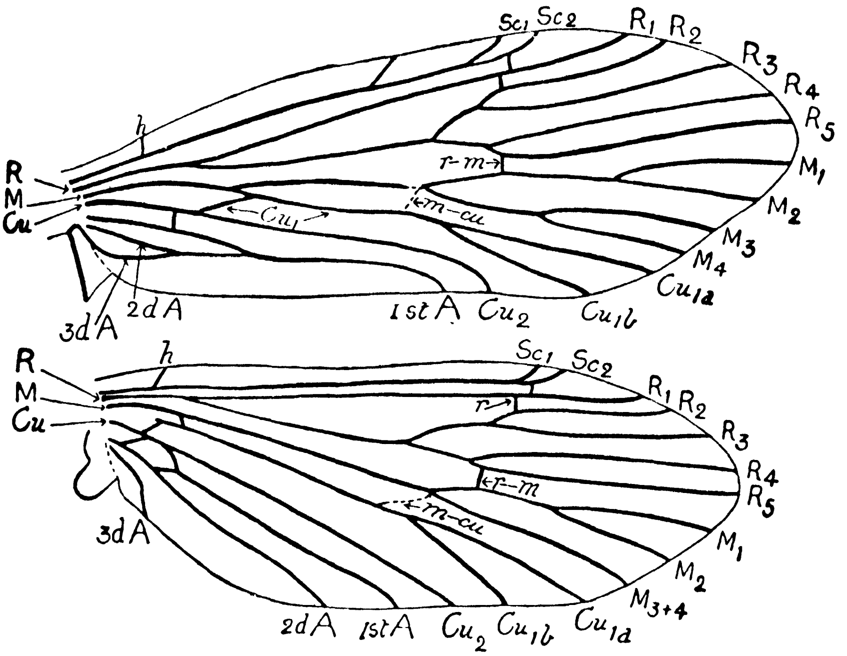

FIG. 408.—RHYACOPHILA FUSCULA, VENATION.
After Comstock, with legend slightly altered.

In the males of species of *Hydroptila* there is an elaborate apparatus of scent-brushes and scent-scales situated at the hinder region of the head and attached to tubes or membranes which are capable of being everted, presumably by means of blood pressure. When not in use these organs are withdrawn into the head (vide Eltringham, 1919).

The internal anatomy of Trichoptera has been very little investigated and only fragmentary accounts exist. The alimentary canal is relatively short with a small stomach, a tubular and slightly coiled intestine, and an expanded rectal chamber: six Malpighian tubes are present. The nervous system, in addition to the usual cephalic centres, consists of 3 thoracic and 7 abdominal ganglia. The testes are simple ovoid sacs and the ovaries consist of numerous polytrophic ovarioles (vide Stitz, *Zool. Jahrb. Anat.*, 20, 1904).

Biology and Metamorphoses.—The early stages of Trichoptera, almost without exception, are passed in fresh water. One or two species develop in brackish or salt water, while the larva of *Enoicyla* is terrestrial, living among moss at the bases of trees in woods. The eggs of caddis flies are laid in water, on aquatic vegetation, on overhanging trees or occasionally far from water (MacLachlan). They are deposited in masses covered by a mucilage which rapidly swells when wetted. The larvæ are the familiar objects known as "caddis worms" and those of the greater number of species form cases or shelters within which they reside. These structures are composed of a basis of silk to which various foreign materials are added. They are commonly tubular in form with an opening at either end. The anterior aperture is wide and through it the head and legs of the contained insect can be protruded. The posterior aperture is usually smaller and is frequently protected by a perforated silken plate. As a rule the larva performs undulatory movements with the abdomen which maintain a current of water in contact with the body, flowing out through the posterior opening of the case. At its hinder extremity the larva is provided with a pair of grappling hooks and it is by means of these organs that it is able to maintain a firm hold of its case, dragging the latter along with it while it crawls about. The variety of cases made by caddis larvæ is very great (vide Fig. 409) and their form and the materials used in their construction are in some cases characteristic of particular species, in others of genera or families. Almost all kinds of material which can be found in the water are utilized by one or other of the species. Leaves, pieces of leaves or stalks, straws, pieces of stick, etc., are often employed while other species select seeds, sand, particles of gravel or the shells of small molluscs. In addition to the case-bearing forms certain other Trichopterous larvæ come under a different category and are, furthermore, structurally different in themselves. In these instances either no habitation is formed at all (ex. *Rhyacophila*) or a silken retreat is formed which is fixed and not portable. These retreats are often common to several larvæ and may be coated with mud or particles of gravel. Species of *Hydropsyche*, *Philopotamus*, *Plectronemia*, etc., which are carnivorous in habit, obtain their food by constructing nets or snares in the water around the mouths of their habitations (vide Wesenberg-Lund, 1911; Noyes, 1914). Such nets are

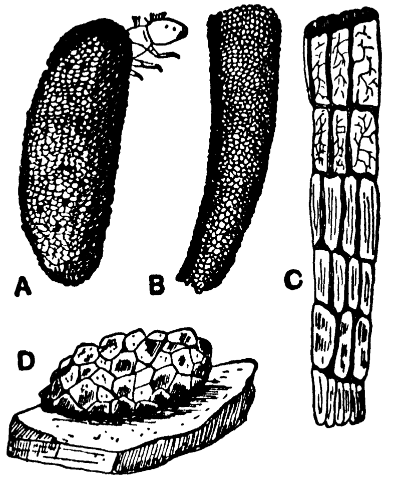

Fig. 409.—Cases of Trichoptera, Magnified.

A, *Hydroptila maclachlani*, case with larva—*after* Klapalek. B, *Odontocerum*, larval case. C, *Phryganea*, larva case. D, *Hydropsyche*, pupal shelter.

composed of strong silken threads which are supported on some available framework such as fragments of leaves or twigs. Water flows freely through the net, but the latter holds back the organisms which serve as food for the caddis larvæ.

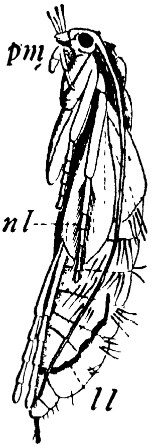

Fig. 410.—A Typical Trichopterous Pupa.

ll, lateral line; *nl*, swimming leg; *pm*, provisional mandibles.

A typical Trichopterous larva has a well-developed chitinized head and very short antennæ (Fig. 411A). Biting mandibles are present and the maxillæ are single-lobed with short 4- or 5-jointed palpi. The labium bears a small terminal median lobe and very much abbreviated palpi. The thoracic terga vary with regard to their degree of chitinization and, in case-bearing larvæ, one or more of the segments bear chitinized dorsal plates. The legs are long and well developed with 1-jointed tarsi, each being terminated by a single claw. The abdomen is typically 10-segmented and generally covered with a membranous cuticle. The first segment, in many species, carries three prominent retractile papillæ, one being dorsal and the remaining two lateral in position. They serve to maintain the insect in position in its case and thereby allow of an even flow of water through the latter. The anal segment in all larvæ bears a pair of short and sometimes jointed appendages: each is terminated by a strong grappling hook and long flexible setæ. The larvæ are apneustic and live submerged, breathing, in most cases, by means of filamentous tracheal gills. The latter are arranged in segmental groups which are commonly disposed in dorsal, lateral, and ventral series along either side of the abdomen. Gills are wanting in newly hatched larvæ and are not acquired until the first or second instar. More rarely gills are absent throughout life and respiration is cutaneous: in some genera a tuft of anal blood gills is present. Most case-bearing larvæ bear a delicate longitudinal cuticular fold on either side of the abdomen: it is beset with fine hairs and is known as the lateral line.

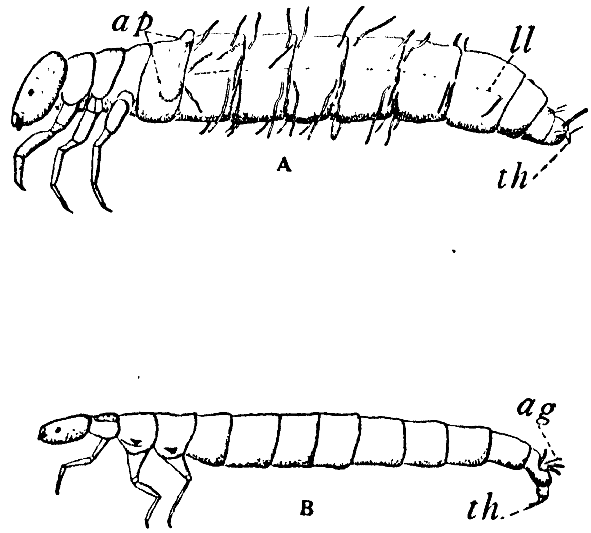

Fig. 411.—Trichopterous Larvæ.

A, Eruciform or case-bearing type. B, Campodeoid or non-case-bearing. *ag*, anal gills; *ap*, abdominal papillae; *ll*, lateral line; *th*, terminal hooks.

Trichopterous larvæ are divisible into two general types. In the first type (eruciform larva of Ulmer) the head is inclined at a marked angle with the rest of the body. Such larvæ are cylindrical in form and construct portable cases. Papillæ are developed on the first abdominal segment and the lateral line and tracheal gills are present. In the second type of larva (campodeoid larva of Ulmer) the body is compressed and the head not inclined at an angle. These larvæ seldom construct transportable cases and both the lateral line and abdominal papillæ are wanting: tracheal gills are seldom present.

The digestive system in Trichopterous larvæ forms a straight tube from the mouth to the anus (vide Betton, 1902; Russ, 1908). The œsophagus leads into a muscular crop which is followed by the stomach: the latter is the most extensive region of the gut and extends from the metathorax into the 6th abdominal segment. The hind intestine is extremely short and is divided into two successive, more or less globular chambers: six Malpighian tubes are present. There are two pairs of salivary glands belonging to the mandibular and maxillary segments respectively (vide Lucas, 1893): a pair of silk glands open on to the labium and these alone persist in the imago, becoming modified during pupation into salivary glands. According to Gilson (1894) the silk glands and associated structures closely resemble those of Lepidopterous larvæ and the silk is produced in a similar manner. Metameric thoracic glands, known as Gilson's glands, occur in many larvæ (vide Henseval, 1896). In *Phryganea* they take the form of a pair of branched tubes in each segment of the thorax: the ducts of a pair unite and open by means of a cannula-like papilla on the mid-ventral line of their segment (Fig. 412). In *Limnophilus* there is a single pair of unbranched glands in the prothorax, those of the other segments being wanting. The thoracic glands have been variously homologized with coxal glands and with nephridia: functionally they are regarded as being accessory organs of excretion. The nervous system is very simple: there are 3 thoracic ganglia and 6 to 8 ganglia are mentioned as being found in the abdominal nerve cord.

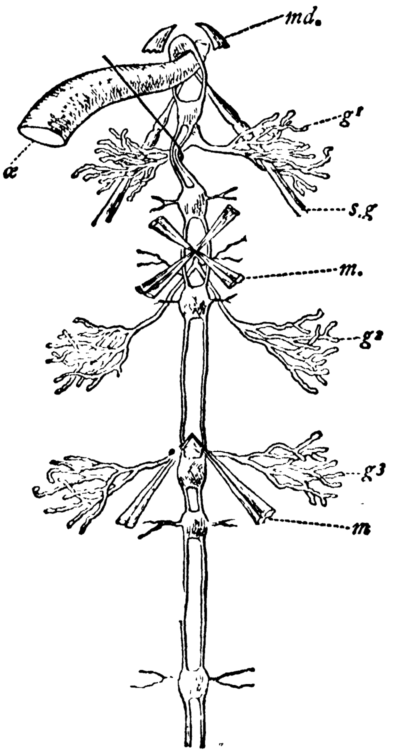

FIG. 412.—THORACIC GLANDS (G^1-G^3) OF THE LARVA OF *PHRYGANEA GRANDIS*.

sg, silk gland; *m*, muscles; *œ*, œsophagus; *md*, mandibles. *After* Gilson, *Journ. Linn. Soc.* 25.

Two distinct types of pupal shelter are prevalent. Before pupation a case-bearing larva shortens its habitation when necessary and fixes it to some object in the water. A silken wall is constructed across either end and these partitions are sometimes strengthened by the addition of minute stones or plant fragments. Due provision is always made for the ingress and egress of the water. The pupa lies free within the case, no cocoon being formed. Most caseless larvæ (*Rhyacophila*, etc.) construct special pupal shelters which take the form of oval cavern-like structures constructed of small stones, sand or other particles. The pupæ in these instances are enclosed in brownish cocoons.

A Trichopterous pupa breathes by means of the persistent larval gills or through the general body surface. It is provided with strong mandibles which are used for biting through the case to allow of the pupa reaching the atmosphere prior to the emergence of the imago. The antennæ, wings, and legs are quite free from the body, and the abdomen is armed with dorsal crochets or spines which enable the pupa to work its way out of its habitation. When the time for the emergence of the imago approaches, the pupa makes an upward passage through the water either by crawling or by swimming. In the former method the legs are clawed and the pupa is enabled to cling to vegetation or other objects. In the case of swimming pupæ a degree of mobility is exhibited which is not attained by the pupæ of any other insects. The middle pair of legs form oars and are provided with hair fringes adapting them to that usage. In some species the pupæ are able to swim freely about at the surface until they find suitable objects to crawl out upon : with the inhabitants of swift streams the imago emerges almost as soon as the pupa reaches the surface.

Certain of the more important features in the biology of the different families may be summarized as follows :—

A. Larvæ of the first type (eruciform)

PHRYGANEIDÆ.—Larvæ mostly in standing water. Cases long and cylindrical, formed of fragments of leaves or fibres arranged in a spiral manner, and open at both ends.

MOLANNIDÆ.—Larvæ in ponds, lakes, or streams, living in shield-like or conical cases composed of sand particles.

LEPTOCERIDÆ.—Larvæ in standing or running water, living in straight or slightly curved cylindrical cases of fine sand, vegetable débris, etc.

ODONTOCERIDÆ.—Larvæ in mountain streams, living in slightly curved cylindrical cases of sand. Hind extremity of case closed by a blackish membrane with a central slit : before pupation the mouth is closed by a single stone.

LIMNOPHILIDÆ.—Larvæ of varied habits, living in both standing and running water. Cases of sand, sticks, leaves, or shells, or of a mixture of several materials.

SERICOSTOMATIDÆ.—Larvæ chiefly in running water : in cases of sand or stones.

B. Larvæ of the second type (campodeoid)

RHYACOPHILIDÆ.—Larvæ in swiftly flowing water : those of *Rhyacophila* live free beneath stones and are often provided with tracheal gills. In *Glossosoma* gills are wanting and the larvæ live in transportable cases of small stones. The pupæ in this family are enclosed in cocoons protected by a shelter composed of gravel or sand particles.

HYDROPTILIDÆ.—Larvæ devoid of tracheal gills and living in standing or flowing water. Their cases are transportable, usually more or less seed-like, sometimes with sand or plant particles attached.

PHILOPOTAMIDÆ, POLYCENTROPIDÆ, PSYCHOMYIDÆ, HYDROPSYCHIDÆ.—In these families the larvæ live in silken non-portable retreats. Tracheal gills are wanting, but anal blood gills are commonly present. Certain of these larvæ are carnivorous and construct silken snares to secure their prey. The pupæ are protected by cavern-like shelters composed of gravel or sand particles.

Among the chief writings on the metamorphoses of Trichoptera are papers by Klapalek (1889-93), Ulmer (1903), Thienemann (1905), Siltala (1907), Lubben (1908), and Lestage (1921). The tables given by Ulmer (1909) for the identification of the larvæ and pupæ are particularly helpful.

Classification.—The following key to the families is adapted from Ulmer (1909): the small family Calamoceratidæ is not included and is unrepresented in the British Isles.

1 (2).—Minute species with long wing fringes: anterior wings closely covered with projecting clubbed hairs. Antennæ not longer than fore-wings: maxillary palpi 5-jointed in both sexes. HYDROPTILIDÆ
2 (1).—Seldom minute species with the wing fringes shorter than width of wing: anterior wings without or with solitary thickened projecting hairs. Antennæ usually longer than fore-wings: maxillary palpi variable.
3 (24).—Maxillary palpi 5-jointed.
4 (11).—Last joint of maxillary palpi ringed, flexible, usually much longer than the rest.
5 (6).—Ocelli present. PHILOPOTAMIDÆ
6 (5).—Ocelli absent.
7 (8).—Anterior tibiæ with 3 spurs. POLYCENTROPIDÆ
8 (7).—Anterior tibiæ with 2 spurs.
9 (10).—R_{2+3} forked in both wings. HYDROPSYCHIDÆ
10 (9).—R_{2+3} fused in both wings. PSYCHOMYIDÆ
11 (4).—Last joint of maxillary palpi not ringed, rarely flexible, sub-equal to other joints.
12 (17).—Ocelli present.
13 (14).—Anterior tibiæ with 1 or no spur: middle tibiæ with 2 or 3 spurs. LIMNOPHILIDÆ (females)
14 (13).—Anterior tibiæ with 2 or 3 spurs: middle tibiæ with 4 spurs.
15 (16).—Two basal joints of maxillary palpi short and thick, third joint much longer and thinner. RHYACOPHILIDÆ
16 (15).—Second joint of maxillary palpi much larger than first. PHRYGANEIDÆ (females)
17 (12).—Ocelli absent.
18 (19).—Discoidal cell absent in both wings. MOLANNIDÆ
19 (18).—Discoidal cell present in fore-wing.
20 (21).—Only upper branch of Rs forked. LEPTOCERIDÆ
21 (20).—Both branches of Rs forked.
22 (23).—Cross-vein between R_1 and R_2 in fore-wing: antennæ much longer than fore-wing. ODONTOCERIDÆ
23 (22).—No cross-vein as in 22: antennæ not much longer than fore-wing. SERICOSTOMATIDÆ (females)
24 (3).—Maxillary palpi with less than 5 joints.
25 (26).—Maxillary palpi 4-jointed: ocelli present. PHRYGANEIDÆ (males)
26 (25).—Maxillary palpi 2- or 3-jointed.
27 (28).—Maxillary palpi scarcely pubescent: ocelli present: anterior tibiæ at most with one spur. LIMNOPHILIDÆ (males)
28 (27).—Maxillary palpi very pubescent: ocelli absent: anterior tibiæ with 2 spurs. SERICOSTOMATIDÆ (males)

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Order 18. LEPIDOPTERA (Butterflies and Moths)

INSECTS WITH TWO PAIRS OF MEMBRANOUS WINGS; CROSS-VEINS FEW IN NUMBER. THE BODY, WINGS, AND APPENDAGES CLOTHED WITH BROAD SCALES. MANDIBLES ALMOST ALWAYS VESTIGIAL OR ABSENT, AND THE PRINCIPAL MOUTH-PARTS GENERALLY REPRESENTED BY A SUCTORIAL PROBOSCIS FORMED BY THE MAXILLÆ. METAMORPHOSIS COMPLETE. LARVÆ ERUCIFORM, PERIPNEUSTIC, FREQUENTLY WITH EIGHT PAIRS OF LIMBS. PUPÆ USUALLY MORE OR LESS OBTECT, AND GENERALLY ENCLOSED IN A COCOON OR AN EARTHEN CELL: WING TRACHEATION COMPLETE.

Lepidoptera are the most familiar and easily recognizable of all insects, and it is in this order that coloration has reached the highest degree of specialization. These insects have always been popular objects for study, and probably not far below 100,000 species have been described. Staudinger and Rebel (1901) enumerated over 9,500 palæarctic species which are represented by more than 2,000 in the British Isles.

On the whole the imagines exhibit a remarkable constancy as regards their fundamental structure, and this uniformity has led to great difficulties in evolving a division of the order into major groups for classificatory purposes. On the other hand, the more superficial or adaptive characters exhibit almost endless variation in the larvæ. As might be anticipated from this structural similarity, the habits of these insects are remarkably uniform. The imagines live entirely upon the juices of flowers, over-ripe fruit, honey-dew and other liquid substances: in a considerable number of species the mouth-parts have atrophied. The larvæ possess masticatory mouth-parts and differ from those of other orders in feeding, with but few exceptions, entirely upon phanerogamic plants.

Economically Lepidoptera are of a great importance in the larva stage. The majority of injurious species devour the foliage and shoots of trees and crops; a smaller number bore into the stems or attack underground parts, and several species are injurious to timber; others attack manufactured goods such as carpets, clothing and their like, while a few are extremely destructive to stored products, including grain, flour, etc. Several predaceous species are enemies of *Tachardia lacca*, and are thereby injurious to lac cultivation, and one or two species live in bee-hives, destroying and fouling the combs. The Saturniidæ and *Bombyx mori*, on the other hand, confer a direct benefit upon man from the fact that they yield silk of commercial value.

Among the more recent general works on the order are those of Seitz (1906 *et seq.*) on the larger Lepidoptera of the world, and Spuler (1901–10) on the European forms. The world's species are listed in the catalogue edited by Wagner (1911, etc.) and those of the palæarctic region by Staudinger and Rebel (1901). The leading treatises on the British species are those of Meyrick (1895), Barrett (1893–1907) and Tutt (1890–1909). The work of the last-mentioned author contains a great deal of biological information but was not completed. Works on the Papilionina are particularly numerous: the species of Europe have been monographed by Lang (1881–4) and other writers; those of North America by Edwards (1868–97) and Scudder (1888–9), both works also containing much general information. Among others, the "Biologia Centrali Americana," volumes by Bingham and by Moore on the oriental species, by Distant on those of Malaysia, and Trimen on those of S. Africa, are important.

The Egg

The eggs of Lepidoptera (vide Tutt, 1899) are roughly divisible into two forms: (1) ovoid or flattened, with the long axis horizontal: in this type the shell is usually only ornamented with rough pittings and rarely with longitudinal ribs; (2) upright and either fusiform, spherical or hemispherical, with the axes either equal, or the vertical axis the longest. The ornamentation is usually more complex and often exhibits a cell-like structure divided by longitudinal ribs.

The *micropyle* is usually placed in a slight depression at one extremity of the horizontal axis of an ovoid type of egg, and at the summit in the upright form. It consists of a number of minute radiating microscopic canals by means of which the spermatozoa gain access into the interior of the egg.

The average number of eggs laid by many species is high, sometimes exceeding 1,000 (*Agrotis fimbria, Zeuzera pyrina*), and they are deposited in a great variety of ways and positions. Certain Hepialids, and also *Charæas graminis*, drop their eggs at random among the herbage on which the larvæ feed. Others, such as *Malacosoma neustria* and *Anisopteryx æscularia*, deposit them in orderly necklace-like rings around the twigs of their respective food-plants. Certain Geometridæ lay them in imbricate groups, while the Adelids are provided with a complex cutting apparatus with which they excise pockets in a leaf. The duration of the egg stage is subject to great variation: in *Acidalia virgularia* it may be as short as two days, but for species which hatch out during the year of deposition 10–30 days may be taken as the usual developmental period. A number of species hibernate in this stage, which is then often of longer duration than the combined larval, pupal, and imaginal periods.

The Larva

Lepidopterous larvæ have a well-developed head, 3 thoracic and 10 evident abdominal segments. Nine pairs of spiracles, borne respectively on the prothoracic and first 8 abdominal segments, are present. In the ***head*** (Figs. 413, 414) the median epicranial suture is well developed and the frons is usually represented by a pair of narrow oblique plates termed the *adfrontals*. Both clypeus and labrum are evident and the typical number of ocelli is 6 which are situated just behind, and a little above, the bases of the short 3-jointed antennæ. The mandibles are powerful and adapted for mastication; in sap-feeding larvæ, however, they are concerned with the laceration of tissues and may even be wanting (*Phyllocnistis*). The maxilla consists of a cardo and stipes; there is usually a single maxillary lobe and the palpi are 2- or 3-jointed organs. The ventral region of the head, between the proximal portions of the maxillæ, is occupied by the labium. The mentum is relatively very large and lightly chitinized; the submentum is usually divided into a pair of triangular sclerites. Distally, the prementum carries a median process or *spinneret*. The labial palpi usually each consist of a principal cylindrical joint and a minute apical joint. On the oral surface of the labium is a median pad or hypopharynx. Paired lobes, which have been interpreted as superlinguæ, overlie the sides of the hypopharynx and have been recognized in *Mnemonica* by Busck and Böving (1914), and by De Gryse (1915) and Heinrich (1918) in other lepidopterous larvæ.

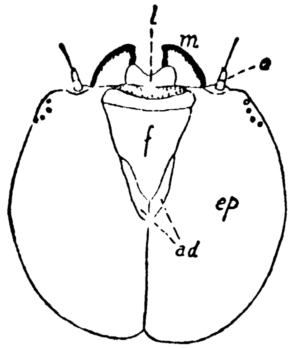

Fig. 413.—*Macrothylacia rubi*, Frontal View of Head of fully-grown Larva.

a, antenna; *ad*, adfrontal sclerites or frons; *f*, clypeus; *ep*, epicranial plate; *l*, labrum; *m*, mandible.

The *thorax* carries a pair of legs on each segment; these are 5-jointed and the terminal joint or tarsus is provided with a single curved claw. The *abdomen* commonly bears five pairs of so-called "prolegs" which are present on segments 3 to 6 and on 10: the first 4 pairs may be termed the abdominal feet and remaining pair the claspers. A typical abdominal leg is a fleshy, more or less conical, retractile projection whose apex or *planta* is rounded or flat. The latter is provided with a series of hooks or crochets which aid the larvæ in locomotion, and to the centre of the planta is attached a muscle by means of which it can be completely inverted.

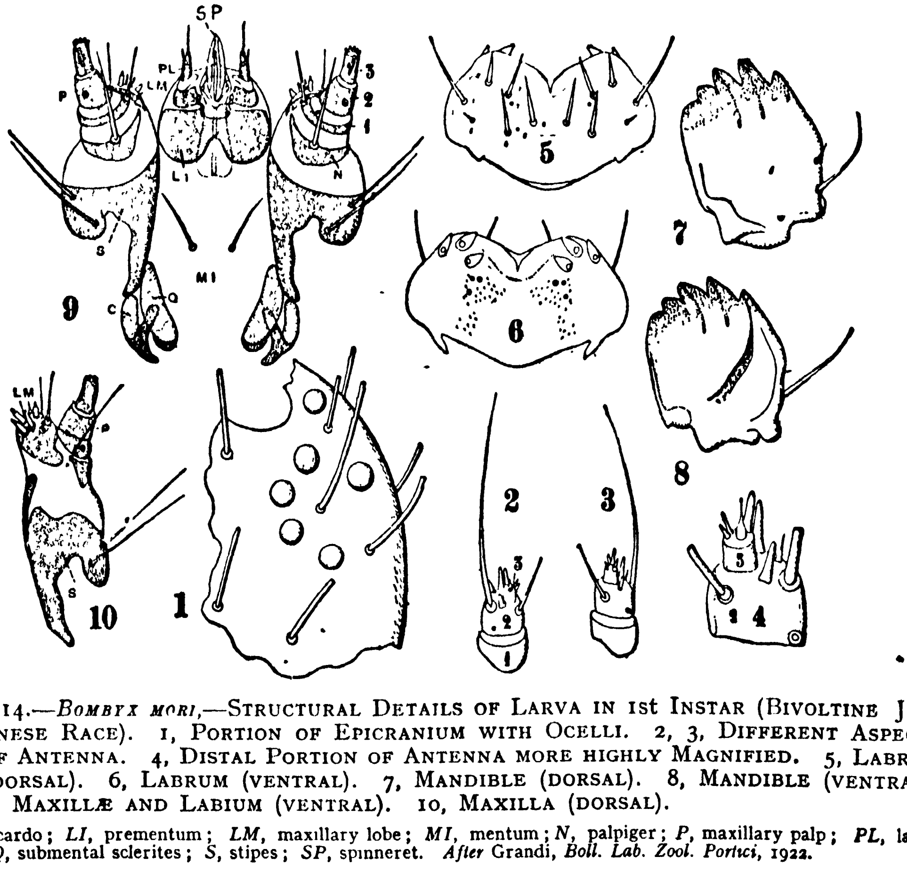

Fig. 414.—*Bombyx mori*,—Structural Details of Larva in 1st Instar (Bivoltine Japanese Race). 1, Portion of Epicranium with Ocelli. 2, 3, Different Aspects of Antenna. 4, Distal Portion of Antenna more highly Magnified. 5, Labrum (dorsal). 6, Labrum (ventral). 7, Mandible (dorsal). 8, Mandible (ventral). 9, Maxillæ and Labium (ventral). 10, Maxilla (dorsal).

C, cardo; *LI*, prementum; *LM*, maxillary lobe; *MI*, mentum; *N*, palpiger; *P*, maxillary palp; *PL*, labial palp; *Q*, submental sclerites; *S*, stipes; *SP*, spinneret. *After* Grandi, *Boll. Lab. Zool. Portici*, 1922.

The arrangement of the crochets is diverse and the variations present afford important classificatory characters (Fig. 415).

In the detailed studies of Fracker (1915) the following terminology is adopted with reference to the arrangement of the crochets. In the most generalized forms the planta bears a complete circle of well-developed hooks, surrounded by several circles of smaller ones. This arrangement is a *multiserial circle* and is found in the *Hepialidæ*, *Hyponomeuta*, etc. When the crochets are absent from the mesial and lateral parts of the circle, as in *Adela*, two transverse *multiserial bands* are formed. When the outer circles of smaller crochets disappear we get a *uniserial circle.* The latter occasionally has crochets of uniform length (*uniordinal*), but more usually they are of two lengths alternating (*biordinal*). When a portion of a uniserial circle is wanting, and the remainder is more than a semicircle in extent, we get a *penellipse* as in the Psychidæ; the gap, moreover, is variable in position. Frequently more than half the circle may be absent, and a *mososeries* results, as in nearly all the higher Lepidoptera excepting the Hesperiadæ.

Departures from the usual number of abdominal limbs are the rule in certain families. Thus in the Geometridæ they are generally present only on the 6th and 10th segments. In the early instars of many Noctuæ the abdominal feet on the 3rd and 4th segments are rudimentary, and the method of progression resembles that of Geometrid larvæ: the limbs of those segments generally attain their full development in a later instar. In the Plusiinæ and several other sub-families, however, they are permanently absent and the looping habit is maintained throughout life. Larvæ of the *Micropteryx* are exceptional in possessing 8 pairs of abdominal limbs. At the opposite extreme are certain leaf-mining larvæ, including those of *Phyllocnistis* and *Eriocrania*, which are totally apodous.

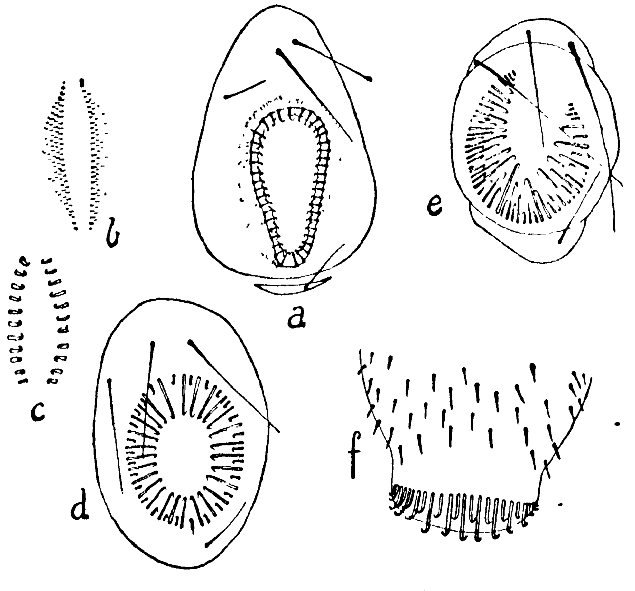

FIG. 415.—ARRANGEMENT OF CROCHETS.

a, multiserial circle; *b*, transverse multiserial bands; *c*, transverse uniserial bands; *d*, biordinal uniserial circle; *e*, penellipse; *f*, biordinal mesoseries. Adapted from Fracker, 1915.

The armature of the body consists of simple hairs or setæ, tubercles of various types, and *verrucæ*: the latter are somewhat elevated portions of the cuticle bearing tufts of setæ. More rarely the body-wall is produced into spinous processes or *scoli* as in the Saturniidæ, or into a median dorsal horn as in the Sphingidæ: other modifications are dealt with under the respective families. The setæ are arranged in a definite manner, and have been extensively studied by Dyar (1894) and Fracker (1915). According to the latter author, the setæ arrangement of the body segments has been derived from a common ancestral type which included 12 primary setæ to each segment. These primary setæ are usually retained in the first instar, but undergo subsequent modifications which afford important taxonomic characters.

Repugnatorial glands are a common feature and there is an extensive literature on the subject. In the Papilionidæ there occur very characteristic organs known as *osmeteria*. An osmeterium consists of a bifurcate protrusible sac which is thrust out through a slit in the 1st thoracic segment. It exhales a distinct odour varying according to the species and in some cases is extremely disagreeable. In many larvæ, including those of the Nymphalidæ, certain Noctuidæ and Notodontidæ a ventral defensive gland is present in the form of an internal sac opening on to the prothoracic sternum, and is capable of discharging a jet of spray. In the Lymantriidæ a pair of eversible glands is present on the dorsum of the 6th and 7th abdominal segments. In many Lycænidæ also there is a dorsal gland on the 7th abdominal segment, its presence being indicated by a transverse slit through which a minute globular vesicle may be protruded. In the Megalopygidæ there are lateral abdominal glands permanently everted, and metamerically arranged (Packard). Many larvæ obtain protection through the possession of *urticating hairs* which bristle with minute lateral points. Whether their irritating properties are due to mechanical action alone, or to the presence of a poisonous secretion, has not been satisfactorily ascertained. These urticating hairs are known to most entomologists who have handled larvæ pertaining to the Lymantriidæ, Lasiocampidæ or Arctiidæ. Such structures evidently produce marked irritation if they come into contact with the epithelial lining of the digestive tracts of an insectivorous bird or mammal. *Glandular hairs* are present in some larvæ and take the form of hollow, smooth setæ. Being filled with a poisonous secretion and extremely liable to fracture, they are capable of causing great irritation and smarting when a larva bearing such setæ is handled. In certain Megalopygidæ these setæ are developed into spines and, according to Packard, the secretion is formed in specialized hypodermal cells situated at their bases.

A very large number of larvæ obtain protection by other means which may be grouped under three chief headings: (1) Concealment. This is evident in case-bearers such as *Coleophora*, the Psychidæ, etc., while in *Nepticula*, *Lithocolletis*, and other Tineina, the larvæ are leaf-miners, and in numerous Tortricidæ they are leaf-rollers. Others construct silken galleries or spin together adjacent leaves as in *Gelechia*, *Pyrameis*, and *Drepana*; in certain Lymantriidæ, and species of *Hyponomeuta*, the larvæ live gregariously in dense silken webs. (2) Protective resemblance. This extensive subject has received a good deal of attention from Poulton and other observers. Protection is attained owing to the remarkable resemblance which many larvæ exhibit to portions of their food-plant, or other objects in their immediate environment. Perhaps the most striking instances are afforded by Geometrid larvæ which bear such a close resemblance to twigs as to render detection often a matter of very great difficulty. The fully-grown larva of *Stauropus fagi* resembles a withered and irregularly curled-up leaf of its food-plant (*Fagus*). Tutt (1899) states that the larva of *Smerinthus ocellatus* bears a remarkable resemblance to a curled apple leaf, its lateral stripes giving an idea of light and shadow on the supposed leaf. The larva of *Anarta myrtilli* with its intricate green pattern is hardly discernible while resting on a twig of heather. A very long list of such instances of protective resemblance might be drawn up, and the phenomenon has probably been induced in the first instance by the presence of chlorophyll in the food-plants, derivatives of which are utilized in the larval coloration. In certain cases the experiments of Poulton tend to show that larval coloration may be due to "phytoscopic," rather than phytophagic influences. In other words, it is the superficial colour of a leaf, for example, rather than its pigmentary substance, that functions as a stimulus in producing differences of coloration under varying environmental conditions. Larvæ of *Catocala*, when subjected to green surroundings, become bluish-green, and in a darkly-coloured environment become bluish-grey. Similarly it has been found that those of *Rumia luteolata* and other Geometridæ tend to exhibit responses of a like nature. We are unacquainted with the mechanism that produces this result, but it is suggested by Poulton that the reflection of light, from the immediate environment of a susceptible larva, produces a nervous response resulting in a physiological change in the accumulation of pigment within the hypodermis. In addition to the writings of this authority an admirable discussion of the subject is given by Tutt (1899). (3) Warning coloration. This is evident in striking colours or patterns which readily catch the eye and their possessors usually feed openly and are distasteful to insectivorous vertebrates.

It has already been mentioned that Lepidopterous larvæ feed almost entirely upon Phanerogamic plants. There is probably not a single family of the latter that is not resorted to by one or more species of these insects. In N. America Scudder states that 52 families are represented in the food-plants of butterflies alone. Exceptions to the habit of feeding upon Phanerogamic plants do occur, but they are not numerous; references thereto will be found in the sections devoted to the Noctuidæ and Tineina.

The number of ecdyses passed through varies greatly in different species and, in some instances, even within the limits of a single species. Edwards (*Psyche*, 1880) finds that four moults is the usual number in N. American butterflies, with an additional moult in hibernating larvæ. Buckler records nine moults in *Nola centonalis*, while in *Acronycta* five is the usual number; Gosse (*Entom.* 1880) finds the same in *Attacus atlas*, and Soule (*Psyche*, 7, p. 191) records a similar number in other Lepidoptera. Species of *Smerinthus* undergo three or four moults, *Sphinx ligustri* six, and three occur in *Callosamia promethea*. *Arctia caia*, on the other hand, may moult seven times—four before hibernation and three after; the number, however, varies between five and eight (Tutt). In a few cases a sexual difference has been noted, the female larva undergoing one more moult than the male, as in *Orgyia*. Chapman observes (*Ent. Month. Mag.* 23) that, in *O. antiqua*, larvæ which moult three times produce males, those which moult five times produce females, and those which moult four times give rise to imagines of both sexes.

The **Internal Anatomy** of Lepidopterous larvae is relatively simple. The *digestive canal* is a straight or almost straight tube, from the mouth to the anus (Fig. 416). The œsophagus is short and frequently enlarged posteriorly (in the mesothorax). The stomach is a tube of wide calibre, extending to the hind margin of the 6th abdominal segment or to the middle of the 7th segment, and is lined by a peritrophic membrane. It is provided with conspicuous muscle bands and, in *Protoparce* for example, its walls are transversely constricted by means of the circular fibres and further divided by six bands of longitudinal muscles. Enteric cœca are rare, but in some species small diverticula are present near the anterior end of the stomach. The hind intestine is always extremely short and devoid of convolutions: in some cases it is divisible into three more or less globular chambers separated by constrictions and probably corresponding to the ileum, colon and rectum. In other larvæ two dilatations (colon and rectum) only are present, while in further examples the hind-gut consists of a single large chamber (vide Bordas, 1911). With very few exceptions, Six Malpighian tubes are present, and they open, on either side, by means of a common duct into a small excretory chamber communicating with the hind-intestine. The common duct bifurcates and one branch subdivides, thus giving rise to three tubes to a side. The *silk glands* are the most conspicuous appendages of the digestive system (Fig. 417). Morphologically they are labial glands homologous with the true salivary glands of other insects. Each gland is in the form of an elongate cylindrical tube of exceedingly variable length, and it lies partly at the side of and partly beneath the digestive canal. These glands are longest in the Saturniidæ and Bombycidæ: thus in *Telea polyphemus* they measure about seven times the length of the body and are complexly folded, while in *Bombyx mori* they are four times the body length, and folded so as to envelop the hinder region of the gut. Anteriorly, each gland is prolonged to form a duct, and the two latter converge and unite to open at the apex of a median cylindrical organ known as the spinneret. The morphology of this structure has not been satisfactorily ascertained, but t appears to be the highly modified ligula. It will be recalled that the labial glands of nsects normally open on the hypopharynx, but in Lepidopterous larvæ their aperture has been carried beyond that organ on to the anterior margin of the labium. Histologically, silk glands consist of a single layer of extraordinarily large secretory cells disposed around a central cavity. The cells have large characteristically branched nuclei, and are limited exteriorly by a peritoneal membrane: internally the gland cavity is lined by chitin, spirally thickened as in tracheæ. The silk ducts possess the same essential histology as the glands, but the epithelial cells are more flattened, and the chitinous lining is closely striated radially (Fig. 155). The spinning apparatus is divisible into two portions, a hinder part, or *thread-press*, and an anterior division known as the *directing tube*. The fluid silk passes into the press which is provided with three pairs of muscles. Action of the latter forces the silk through the directing tube, very much as wire is made by molten iron

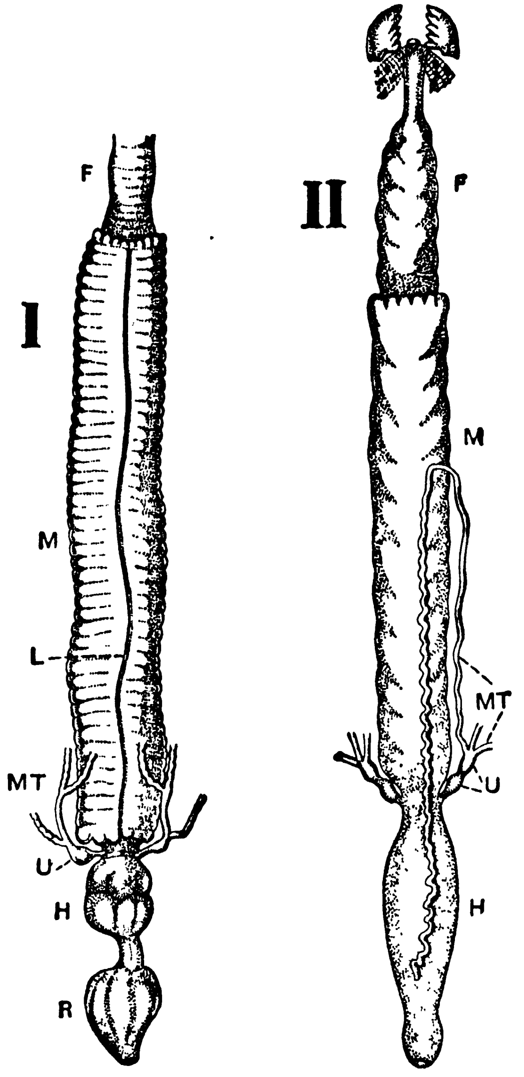

FIG. 416.—ALIMENTARY CANAL OF LARVA OF I, *ACHERONTIA ATROPOS*; II, *SPILOSOMA FULIGINOSA*.

F, fore-intestine; *H*, hind-intestine; *L*, dorsal longitudinal muscle band; *M*, mid-intestine; *MT*, malpighian tubes; *R*, rectum; *U*, excretory chamber. *After* Bordas, 1911.

being driven through an iron plate, perforated by two fine holes (Packard). The entire spinning apparatus lies within the spinneret, and the thread as it issues from the aperture of the latter is in the form of a double ribbon-like band. Associated with the silk glands in most species is a pair of *accessory glands*, often improperly termed Filippi's glands, notwithstanding the fact that they were recognized by Lyonnet so long ago as 1762 (Bordas). They are paired organs, often voluminous, and each opens by a separate duct into the silk duct of its side. In *Arctia caia* and *Cydia pomonella* they are rudimentary, and reduced to a group of follicles surrounding the silk duct. Among the Sphingidæ they are also rudimentary or entirely absent. The function of these glands is to secrete a substance of a liquid or viscid nature which enables the two threads to adhere and, at the same time, facilitates the process of hardening. *Mandibular glands* (Fig. 153) are present in almost all Lepidopterous larvæ, and are situated in the thorax one on either side of the fore-intestine. They communicate with the buccal cavity by means of a pore placed on the inner side of the base of each mandible. As a rule they are tubular and often of considerable length, but in *Papilio alexenor* and *Stauropus fagi* they are short and sac-like. Histologically they consist of the same layers as the silk glands and their nuclei are lobed or irregular in form. Functionally they are salivary glands and, in some cases, according to Bordas, they may exercise a defensive rôle also.

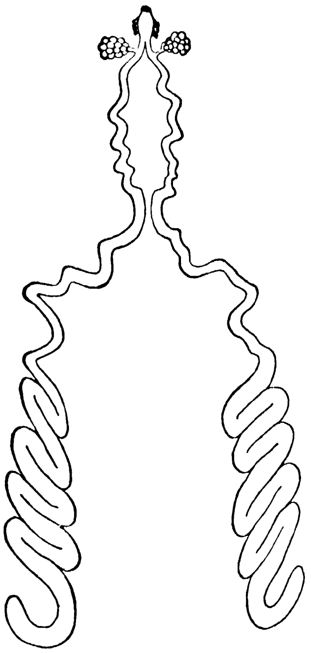

FIG. 417.—SPINNING GLANDS WITH SMALL ACINOSE ACCESSORY GLANDS OF THE LARVA OF *SATURNIA PYRI*. *After* Bordas, 1910.

The *nervous system* is subject to but little variation. In addition to the usual cephalic ganglia the central nervous system consists of three thoracic and seven or eight abdominal ganglia. The connectives between the meso- and meta-thoracic ganglia are, typically, double and widely separated, but those uniting the remaining ventral ganglia appear as single cords. As a rule, the 7th and 8th abdominal ganglia are intimately united owing to the elimination of the connective between them. In *Sphida* the number of paired nerves arising from the terminal ganglion suggests that three or more nerve centres have undergone coalescence (Du Porte): in *Cossus* the 7th and 8th abdominal ganglia are separate and united by a short connective (Brandt). The *dorsal vessel* extends from the 8th abdominal segment into the 1st segment, or the commencement of the metathorax, and from there it is continued as the *aorta* into the head. According to Newport there are nine chambers separated by eight pairs of lateral ostia. The *reproductive organs* take the form of a pair of small ovoid bodies situated in the 5th abdominal segment and in close relation with the dorsal vessel on either side. They are present in the newly hatched larvæ and undergo a certain amount of differentiation during later instars. The ovaries are slightly larger than the testes and may also be recognized histologically by the rudiments of ovarioles.

The Literature on lepidopterous larvæ is very extensive : larvæ of the British species are illustrated by Buckler (1885-99), while for the European species reference should be made to the work of Hofmann (1893). For a general account of the external structure of the larvæ of the order the works of Tutt (1899) and Forbes (1910) are useful : for the Papilionina vide Scudder (1889). For the larval characteristics of the different families and diagnostic keys, vide Dyar (1894), Forbes (1910) and Fracker (1915). The internal anatomy has been mainly studied in isolated species, notably in *Cossus* by Lyonnet (1762), *Bombyx mori* by Blanc (*Trav. Lab. Soie,* 1889-90) and others, and *Protoparce* by Peterson (1912). The digestive system and Malpighian tubes have been extensively studied by Bordas (1911) ; and many investigators, more especially Helm (1876), Gilson (1890) and Bordas (1910), have devoted attention to the silk and other glands. The nervous system has been studied by Newport (1832), Brandt (1879), Cattie (1881) and Du Porte (1915).

The Pupa

The change from the larva to the pupa usually first becomes evident by cessation of feeding. In many cases the larvæ desert the food-plant and wander in search of a suitable site in which to undergo the transformation. The contents of the digestive canal are voided and the larval skin loses much of its characteristic colour, becoming darker and wrinkled. The body becomes contracted and distended, the hypodermis secretes a fresh layer of chitin beneath the old cuticle, and ecdysis is greatly aided by the secretion of the exuvial glands which gradually loosens the two layers. When the latter process is complete, dehiscence of the larval skin takes place along the middle of dorsal aspect of the thorax, and the exuvia is gradually slipped off from behind, thus liberating the pupa. In the majority of species pupation takes place in a cocoon of some description, which is constructed by the larva. It may be composed of silk as in Bombycidæ, Saturniidæ, Lasiocampidæ, etc. ; or of leaves drawn together by a silken meshwork, or of a mixture of silk and various foreign particles. In other cases, as in *Dicranura* and *Cerura,* the cocoon is formed of gnawed fragments of wood agglutinated together by means of a fluid secretion which quickly hardens. Also, in the construction of the earthen cells of many Noctuidæ the soil particles are cemented together by a fluid secretion, and no silk appears to be utilized. Among the Papilionina the pupa is very frequently naked and protectively coloured, and suspended by the caudal extremity which is hooked on to a small pad of silk : the latter, and the silken girdle which is often present, may possibly represent the last vestige of a cocoon. The usual division of the body into head, thorax and abdomen is easily recognized in the pupa and the general external structure has been studied by Poulton (1890-91), Packard (1895). Chapman (1893-96), Mosher (1916) and others (vide Figs. 203 and 418).

The Head.—The *vertex* forms the dorsal area of the head behind the epicranial suture while the region anterior to the latter is the *fronto-clypeus.* In a few generalized forms, however, the frons and clypeus are separately demarcated. Invaginations of the anterior arms of the *tentorium* are evident as small pores or slit-like openings associated with the lateral margins of the clypeus. The *labrum* is usually very distinct but a clypeo-labral suture appears seldom to be developed : in many families the labrum bears lateral projections or *pilifers* and according to Mosher they are notably conspicuous in the Pyralidæ and Papilionoidea. Definite *genæ* are rarely evident except among the Homoneura. The *eyes* are always prominent and are divided into smooth and sculptured portions, the former being regarded as the true pupal eye. The *antennæ* exhibit less marked sexual differences than in the imago and, in *Saturnia pavonia* for example, the pupal differences are extremely small in the two sexes, notwithstanding their divergence in the imago. *Mandibles* are only functional among certain of the Micropterygidæ: in *Eriocrania* they are very large and are used by the pupa to cut its way through the cocoon. In other families they are only represented by small elevated areas. The *maxillæ* are exceedingly variable, and attain their greatest development in certain Sphingidæ where their great length is accommodated by their becoming looped to form the familiar " jug-handle " appendage. *Maxillary palpi* are wanting in certain groups, notably in the Cossidæ, Hepialidæ and in butterflies. *Labial palpi* are visible in many pupæ but, in others, they are almost entirely concealed by the maxillæ.

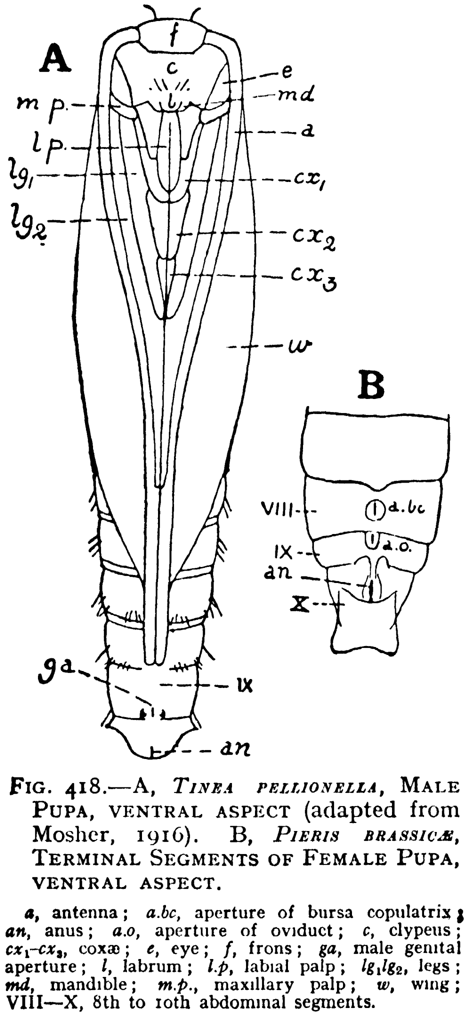

FIG. 418.—A, *Tinea pellionella*, MALE PUPA, VENTRAL ASPECT (adapted from Mosher, 1916). B, *Pieris brassicæ*, TERMINAL SEGMENTS OF FEMALE PUPA, VENTRAL ASPECT.

a, antenna; *a.bc*, aperture of bursa copulatrix; *an*, anus; *a.o*, aperture of oviduct; *c*, clypeus; *cx*$_1$–*cx*$_3$, coxæ; *e*, eye; *f*, frons; *ga*, male genital aperture; *l*, labrum; *l.p*, labial palp; *lg*$_1$*lg*$_2$, legs; *md*, mandible; *m.p.*, maxillary palp; *w*, wing; VIII—X, 8th to 10th abdominal segments.

The Thorax.—The three segments are distinct on the dorsum but ventrally they are concealed by the appendages. The anterior pair of wings almost entirely conceals the posterior pair, except for a narrow strip along the dorsal margin of the latter. Among the apterous or subapterous females of certain genera the pupal wings are likewise less developed than in the male. In *Hybernia defoliaria* and *Nyssia zonaria* the sexual divergence is but little marked in the pupa, although the female imagines are almost apterous. In such forms as *Orgyia*, and the Psychidæ, the degeneration appears to be sufficiently ancient to have caused a corresponding reduction of the wings of the female pupæ. The thoracic *spiracles* consist of a single pair placed between the pro- and meso-thorax, towards the dorsal aspect.

The Abdomen.—Ten abdominal segments are present and a certain number are always fixed and immovable. The greatest number of free segments are found in the more generalized forms, thus in *Mnemonica* all the segments are movable excepting the last three (Mosher). In the Hepialidæ and Psychidæ the 1st segment is fixed and segments 2 to 7 are free in the male and 2 to 6 in the female; in the Cossidæ the first two abdominal segments are fixed and consequently the movable segments are 3 to 7 in the male and 3 to 6 in the female; in the Noctuidæ, Geometridæ, Sphingidæ, etc., the only free segments are the 4th, 5th and 6th in both sexes, while among certain of the butterflies all the segments are immovable. *Spiracles* are present on the first eight segments: the first pair is usually covered by the wings and the last pair is vestigial. In male pupæ the genital aperture is situated on the 9th sternum and in the female there is either a single common aperture on the 8th sternum (10th sternum in *Micropteryx* according to Chapman) or, more usually, two apertures which are associated with the 8th and 9th sterna. These openings in some cases become confluent and represent those of the bursa copulatrix and oviduct respectively. The anus is carried on the caudal margin of the 10th segment, and this somite is produced to form the *cremaster*, which is the homologue of the suranal plate of the larva. It is an organ of attachment and exhibits many modifications: it may take the form of a pointed spine or of hooklets, and the latter may be grouped together, or scattered irregularly over the surface of the anal segment. In many of the more generalized families the cremaster is absent, while among the butterflies, with their suspended pupæ, it is particularly well developed.

Internal Structure.—The internal anatomy differs in important features both from that of the larva and imago but more closely approaches the latter. The digestive system has undergone extensive modifications as compared with that of the larva; the œsophagus is long and narrow and the stomach greatly reduced in size. The food-reservoir is undeveloped and the hind-intestine less convoluted than in the imago. The larval silk glands have atrophied, and the salivary glands of the imago replace them. The changes undergone by the nervous system have been studied in great detail by Newport, and briefly it may be said that it undergoes a gradual process of concentration during about the first 60 hours of pupal life. By that time its whole arrangement is very nearly as it exists in the imago. The developmental changes undergone by the genital system are dealt with on a later page.

Types of Pupæ and Method of Emergence from the Cocoon.—Chapman (1893) divides Lepidopterous pupæ into two main groups, the Incompletæ and Obtectæ. The *pupæ incompletæ* have the appendages often partially free and more than three of the abdominal segments are mobile. Dehiscence is accompanied by the freeing of segments and appendages previously fixed, and the pupæ exhibit considerable power of motion, usually emerging from the cocoon to allow of the escape of the imago. They are provided with a varied armature of hooks, processes and spines to facilitate the process. Many species also work their way to the surface of the ground, or to the entrance of the larval gallery in the case of those whose larvæ are internal feeders. In the Micropterygidæ the pupæ have a larger number of free segments than in any other family and are *pupæ liberæ*. *Eriocrania*, *Sabatinca* and *Mnemonica* are also unique among Lepidoptera in possessing mandibles for cutting through the cocoon. These organs, assisted by the mobility of the abdominal segments, enable the pupa to free itself and pass through any superincumbent earth to the surface. Most other pupæ incompletæ possess some kind of hard process adapted for tearing open the cocoon. This *cocoon cutter*, as it may be termed, is well seen in *Lithocolletis hamadryadella* and according to Packard there are rough knobs or slight projections answering the same purpose in the *Hepialidæ*, *Megalopyge*, *Zeuzera* and in *Datana*. The *pupæ obtectæ* represent a more highly specialized type: they are smooth and rounded and the only free segments in both sexes are the 4th, 5th and 6th. Dehiscence takes place by an irregular fracture, the pupa rarely emerges from the cocoon, and a cremaster is generally present. This pupa is prevalen in all the higher Lepidoptera, and exhibits a hard exterior, the appendages being all soldered down to form a smooth surface. The areas which are hidden are covered by a delicate pellicle and there is no separation of the appendages after emergence. Certain species (*Saturnia pavonia, Chœrocampa elpenor*) have retained the habit of pupal emergence, but in other forms the presence of the cremaster and the reduced mobility of the abdominal segments usually preclude it. Many different methods have been adopted to allow of the freeing of the imago. These may consist of weak places in the cocoon, a particular arrangement of the silk to allow of easy egress (*Saturnia pavonia*), a softening fluid applied by the emerging insect (certain Saturniids, *Dicranura*), provisional imaginal spines (Attacine moths), etc.

THE IMAGO

External Anatomy

THE HEAD (Fig. 419).—The greater part of the head is formed by the epicranium which carries laterally the large globular *compound eyes*. The *ocelli* are two in number and lie close behind the latter: they are seldom conspicuous, and generally much concealed by scales or often absent. The anterior region of the head is occupied by the *fronto-clypeus* which is frequently demarcated from the epicranium by means of a transverse suture. In a few cases (*Acherontia* according to Berlese) the clypeus is separately differentiated from the frons as a narrow band-like sclerite. The *labrum* is narrow and pointed in *Micropteryx* and its allies but forms a short transverse plate in other Lepidoptera. It is provided with a small pointed median projection which is usually regarded as an extension of the *epipharynx*. Between the fronto-clypeus and the eyes are the narrow *genæ* and, when mandibular rudiments are present, they either articulate or fuse with the latter sclerites. The *antennæ* (vide Jordan, *Novit. Zool.* 5) are composed of an indefinite number of joints and vary greatly in length and structure. In the male they frequently show an increased development as compared with the female which is particularly well exhibited in the Saturniidæ. They are generally scaled dorsally and very often ventrally also: in some cases scales are absent as in the Saturniidæ and many Papilionina.

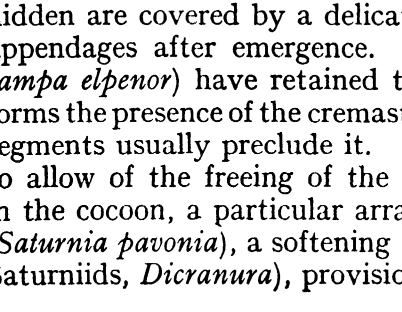

FIG. 419.—FRONTAL VIEW OF THE HEAD OF A LEPIDOPTERON.
After J. B. Smith.

MOUTH-PARTS.—In the majority of Lepidoptera, mandibles are totally wanting and the maxillæ are highly modified to form a suctorial proboscis. The latter is composed of the two greatly elongated galeæ, each being channelled along its inner face, and the two are held together by means of hooks and interlocking spines. In this manner the combined grooves form a tube through which liquid food is imbibed. The laciniæ are either entirely atrophied or, according to Berlese, rudiments thereof may be embodied in the base of the proboscis. When fully developed, the maxillary palpi are 5- or 6-jointed and usually more or less folded, as in the Tineidæ; in the great majority of Lepidoptera they are either much reduced or wanting, their functions presumably being assumed by the labial palpi. Among Noctuidæ they are 2- to 3-jointed; in the Sphingidæ, Papilionoidea and most Geometridæ they are single-jointed (Walter, 1884). The labium is reduced to a small plate on the ventral aspect of the mouth: its palpi are normally 3-jointed and vary greatly in size, shape and scaling. A hypopharynx is present on the floor of the mouth and in *Danais* it is provided with gustatory papillæ.

When not in use the proboscis is spirally coiled and stowed away beneath the thorax: it presents an extraordinary variation in length, attaining its maximum in the Sphingidæ. In *Danais*, according to Burgess (1880), each half of the proboscis is seen to be composed of an immense number of chitinous rings, which are incomplete since they are absent from its inner or grooved aspect. These rings are separated by intervening bands of membrane which admit of the spiral coiling of the organ. Each ring is made up of a row of quadrangular plates which are provided with spine-like processes directed towards the proboscis channel, hence the plates are somewhat nail-like in form. Scattered over the surface of the proboscis, and more especially at the apex, are small circular plates each bearing a minute central papilla, which are perhaps tactile in function. According to Breitenbach they are often developed into denticulate spines which enable the proboscis to lacerate the tissues of fruit and imbibe their juices: this condition is particularly well exhibited in *Aletia xylina*. The interior of each half of the proboscis is hollow and occupied throughout its length by a nerve and a trachea, but the bulk of its cavity accommodates two sets of muscles which diagonally cross it. From their attachment the action of these muscles would result in shortening the posterior wall of the maxilla and produce the spiral coiling of the organ. The method of extension of the latter does not appear to be clearly understood, and it has been variously suggested to take place by means of its own elasticity or by blood pressure. Burgess suggests that we have failed to interpret some muscular mechanism for the purpose.

In some Lepidoptera (*Orgyia*, *Zeuzera*, etc.) the proboscis is reduced and non-functional, the two galeæ remaining separate; in many others the galeæ are represented by two minute papillæ (*Hepialus*) or entirely atrophied. In the reduced or atrophied condition it is evident that no food can be imbibed and the mouth may be wanting also (Saturniidæ), but the subject is in need of fuller investigation.

The mouth-parts are exhibited in their most primitive form in *Sabatinca* (Tillyard, 1923) where they are clearly of the mandibulate rather than the haustellate type. The mandibles are functional dentate organs, with evident ginglymus and condyle, and movable by means of well developed abductor and adductor muscles. The maxillæ are entirely in conformity with the mandibles: both cardo and stipes are evident, the galea is short and 2-jointed, the lacinia blade-like, and the palpi are long and 5-jointed. In the labium, however, there is no ligula and lobes formerly regarded as paraglossæ are in reality processes of the palpi (Tillyard): the basal sclerites are represented by a single mental plate. The hypopharynx in *M. ammanella* is laterally provided with small accessory pieces which are regarded by Busck and Boving as the superlinguæ. In *Eriocrania* the mandibles are non-dentate and in *Mnemonica* they are unchitinized with the ginglymus and condyle rudimentary: proof that these are true mandibles is afforded by the fact that they lie within those of the pupa. In both the above genera the laciniæ are lost, and the 2-jointed galeæ are greatly elongated. The terminal joint of the galea of either side is apposed to that of its fellow, thus exhibiting the first step in the formation of the Lepidopterous proboscis. In addition to the Micropterygidæ, vestigial mandibles are stated to be present by Petersen in *Hepialus*: they also occur in various Tineoids including *Argyresthia*, *Tinea*, *Tineola* and *Hyponomeuta* (Walter, 1885).

According to Kellogg (1895) in *Protoparce carolina* conspicuous mandibular rudiments are present, being strongly chitinized and slightly dentate at their apices. They plainly arise from the genæ and a faint articulating suture is visible. The so-called mandibular rudiments of *Danais*, and other of the higher Lepidoptera, are lateral projections of the labrum and are termed by Kellogg the pilifers: as that authority has pointed out, both mandibles and pilifers may occur together as in *Protoparce*. The maxillæ of *Pronuba* are exceptional in exhibiting sexual dimorphism: in the male they are normal but the galeæ are quite separate, and in the female there is an elongate inner lobe often known as the maxillary tentacle. The two latter organs are adapted for holding a large mass of pollen beneath the head: their morphology is doubtful and it has been suggested that they are the greatly produced palpifers.

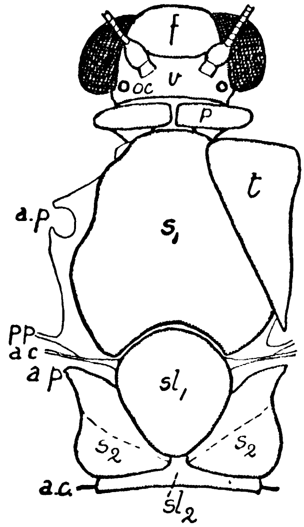

FIG. 420.—DORSAL VIEW OF HEAD AND THORAX OF *AGROTIS PRONUBA* (LEFT TEGULA REMOVED).

a.c, axillary cord; *a.p*, anterior wing process; *f*, frons; *oc*, ocellus; *p*, patagium; *pp*, posterior wing process; s_1, mesoscutum; sl_1, mesoscutellum; s_2, metascutum; sl_2, metascutellum; *t*, tegula; *v*, vertex.

In the THORAX (Fig. 420) the prothorax is evident in the lower forms but compressed and reduced in all the higher families where it assumes the form of a collar. It frequently carries a pair of small lateral processes or *patagia* which are peculiar to Lepidoptera and appear as thin, lobe-like, erectile expansions, well developed in many Noctuidæ (e.g. *Agrotis*). These structures are often confused with tegulæ but the latter are never borne on the prothorax. The mesothorax is the largest and most prominent segment of the three; its tergum consists of a narrow band-like prescutum, a very large, longitudinally divided scutum and a well-developed more or less rhomboidal scutellum. *Tegulæ* are particularly well developed and very characteristic of the order; each is carried on a special tegular plate of the notum supported by means of a tegular arm arising from the base of the pleural wing process (Snodgrass). The metathorax is relatively small as compared with the previous segment; Snodgrass finds that in *Phassus* (Hepialidæ), however, it is larger and more like the mesothorax than is usual among the higher insects. In most other Lepidoptera it is very much shortened antero-posteriorly and greatly reduced. A post-scutellum is present in both the meso- and metathorax but largely concealed.

With regard to the LEGS a meron is present in relation with the meso- and meta-thoracic coxæ and, as a rule, the coxæ have but little mobility upon the pleuron, the principal movement of the base of the leg being in the articulation between the coxa and trochanter (Snodgrass). The anterior legs exhibit special features in certain families of Papilionoidea and are reduced and modified so as to become useless for walking, either in the male only (Erycinidæ) or in both sexes (Nymphalidæ). The anterior tibiæ are comparatively short in most Lepidoptera and in certain families they are provided on the inner surface with a peculiar lamellate spur ("epiphysis") which is regarded by Haase as the vestige of an organ formerly developed for cleaning the antennæ. Frequently in the male the posterior tibiæ (more rarely the middle pair) are provided with an expansile tuft of hair which is located in a groove and functions as a scent-producing organ. The tarsi are normally 5-jointed, the first joint being much the longest and in the males of certain Lycænidæ it is conspicuously swollen. In the Pieridæ the claws are exceptional in being cleft or bifid, and among

Lycænidæ either one or both claws are wanting in the male. In the degenerate females of the Psychidæ the legs have atrophied.

WINGS.—The most characteristic feature is the covering of overlapping scales which are, morphologically, flattened and highly modified macrotrichia. Transitional stages between the latter and short broad scales are readily observable and the identity of the two types of structures is clearly established. Thus, in *Prototheora* Meyr. Tillyard mentions that macrotrichia remain in an unmodified condition on the veins. The scales on the wing membrane lying closest to the veins are linear and narrow, becoming shorter and broader the further they are away from a vein. Microtrichia (fixed hairs of Kellogg; aculei of Busck) are present on the wing-membrane in the Homoneura as well as in the more archaic families of the Heteroneura.

The innervation of the wings has been studied by Vogel (1911) who finds that each wing is supplied by three nerve branches whose fibres are ultimately distributed to the various sensory organs present. Vogel (1912) recognizes four types of the latter, each organ having a sensory cell at its base. Possibly tactile are sensory scales and setæ, while certain papillæ suggest, on account of their structure, an orientating function. At the bases of the wings are still more problematical structures which are termed chordotonal organs and, in some cases, a well developed "tympanal area" is associated with them, which suggests that they may have some concern with the perception of sound. The scales of Lepidoptera do not strengthen the wings or aid the insects in flight. The vast majority of these structures are simply colour-bearing organs which have been developed under the influence of natural selection. They are secreted by evaginated and greatly enlarged hypodermal cells—the formative cells of Semper (Fig. 421). Their structure and development have been studied in considerable detail, more especially by Mayer (1896). Each scale is provided with a short pedicel which fits into a minute socket in the wing membrane. In the more primitive forms they are irregularly scattered but in the Papilionina, for example, a regular arrangement is very noticeable. On its exposed or outer surface, each scale is ornamented with longitudinal ridges or striæ, often with transverse trabeculæ between them. These ridges are in the form of longitudinal thickenings of the outer scale-wall, and their presence imparts rigidity very much after the manner of the

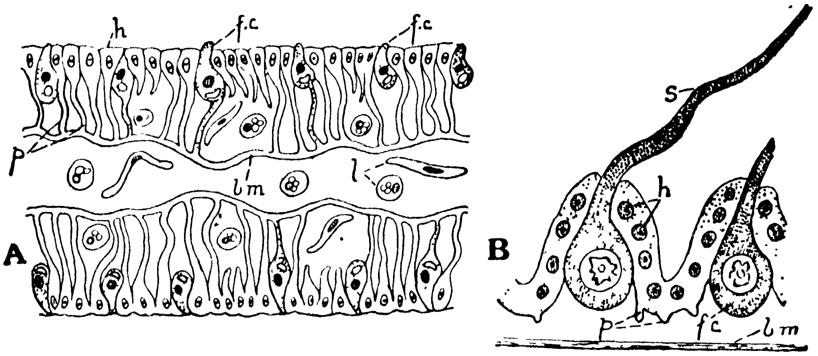

FIG. 421.—A, PORTION OF A YOUNG PUPAL WING OF *VANESSA ANTIOPA* IN LONGITUDINAL SECTION. B, THE SAME OF *DANAIS PLEXIPPUS*, ABOUT 8 OR 9 DAYS BEFORE EMERGENCE.

h, hypodermis; *f.c.*, formative cell of scale; *l*, leucocytes; *bm*, basement membrane; *p*, processes of hypoderm cells; *s*, developing scale. *After* Mayer, *Bull. Mus. Harvard*, 1896.

corrugations on a sheet of roofing iron. In many cases these striæ are extremely fine. and Kellogg (1894) found that in a species of *Morpho* they are placed from ·0007 to ·00072 mm. apart, or at the rate of 35,000 to the inch, and are responsible for producing beautiful iridescent colours (vide p. 11). Seen in microtome sections scales are greatly flattened hollow sacs (Fig. 423) strengthened by minute transverse bars. Although they may only contain air, in the majority of cases a layer of pigment is enclosed between the two walls. In surface view they exhibit a wide range of variation of both form and sculpturing. In the males of various Lepidoptera groups of more specialized scales or *androconia* (plumules) occur on the upper surface of the wings and likewise assume very varied shapes (Fig. 422). They are found either scattered over portions of the wings, or in limited areas such as the "brand" or discal patch of *Pamphilus*, the discal patch of certain Lycænids, as well as on folds of the wings and other situations. Physiologically they are scent scales which serve as the outlets of odoriferous glands (Thomas, *Amer. Nat.* 1893); they are often fringed distally, with each tip of the fringe finely divided, thus probably ensuring the ready diffusion of the odour so characteristic of many Lepidoptera. Among the Danaine butterflies (Nymphalidæ) a glandular scent patch is present on each hind-wing and the odoriferous secretion is exuded at the surface of the wing by means of cuticular "cups." These latter are provided with a covering membrane pierced in the centre by a minute pore. Each cup is protected by a small scale differing from normal wing scales in size and shape (Eltringham, 1915). In *Amauris niavius* the insect has been observed to brush the odoriferous area with the anal tuft of hairs which thus acquires some of the characteristic odour. Included in the anal tuft are numerous delicate chitinous filaments having the property of breaking up transversely into minute particles thus forming a kind of dust which presumably assists in the diffusion of the scent. It is noteworthy that Dixey has shown that in certain Pieridæ an alcoholic extract may be made from the wings and it possesses the same odour as the species concerned.

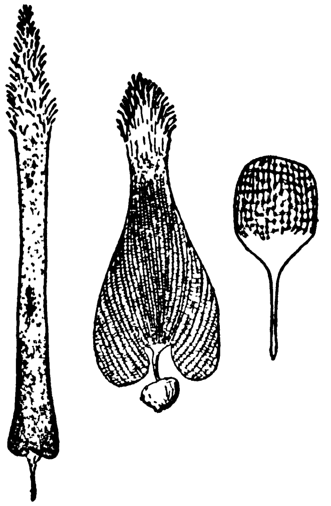

Fig. 422. — Androconia of Male Butterflies.

From Comstock *after* Kellogg.

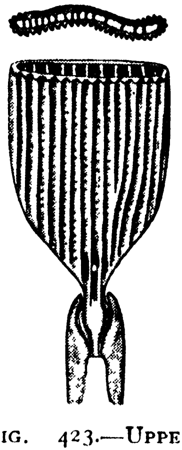

Fig. 423.—Upper (i.e. Exposed) Portion of a Scale of *Danais plexippus* with the Distal Portion cut away to show the Cross Bars: above is seen a Scale in Transverse Section.

After Mayer, *loc. cit.*, 1896.

With regard to the VENATION (Figs. 425, 426) wherever specialization is evident it has been the result of the atrophy or coalescence of veins and not by addition. Throughout the order the principal cross veins are few in number and vein M_4 is distally fused with Cu_{1a}. The researches of Tillyard (1919) provide strong evidence indicating that 1A of Comstock is in reality Cu_2, a conclusion which has been adopted in the present work. One of the most characteristic features of the lepidopterous wing is the *trigamma* or 3-pronged fork, whose prongs are represented by M_3, Cu_{1a} and Cu_{1b} and whose base completes the closure of cell M or its regional equivalent. Among the Cossidæ the stem R_{4+5} (chorda of Turner, 1918) divides the cell R into the basal cell 1st R, and an apical cell 2nd R (areole of Turner). In the vast majority of Lepidoptera, however, the stem R_{4+5} has atrophied and also the main stem M. This condition has resulted in the formation of a single enormous discal cell on account of cells R+M+1st M_2 thus becoming confluent.

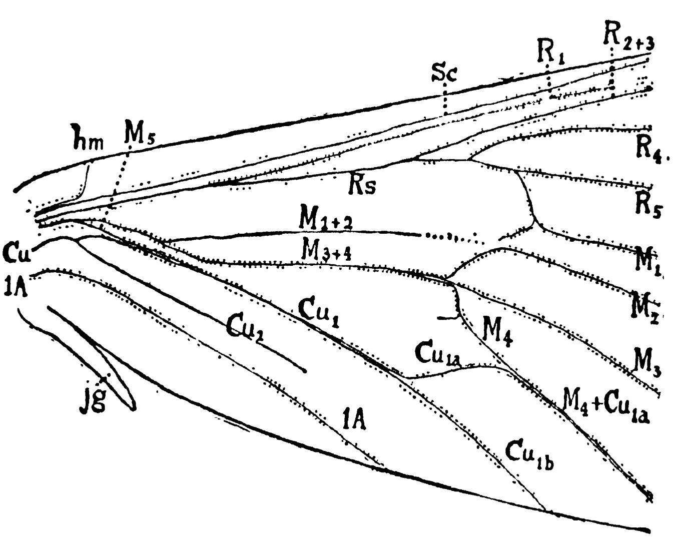

FIG. 424.—BASAL PART OF FOREWING OF *CHARAGIA* (HEPIALIDÆ) SHOWING VENATION (DOUBLE DOTTED LINES) AND TRACHEATION × 4.

After Tillyard, *Proc. Linn. Soc. N.S.W.* 44, *pt.* 3.

The most primitive type of venation is found in the family Micropterygidæ of the Homoneura where that of both pairs of wings is closely alike (Fig. 425). Most of the archaic features are exhibited in *Mnemonica* Meyr. in which Sc and R_1 are separate in both pairs of wings, and bifurcated in the fore-wings; Rs is 3-branched in the hind-wings and the three branches of Cu are complete. In the family Hepialidæ both Sc and R_1, although almost always distinct, are typically unbranched and there is a considerable reduction or partial atrophy of Cu_2 in one or both pairs of wings.

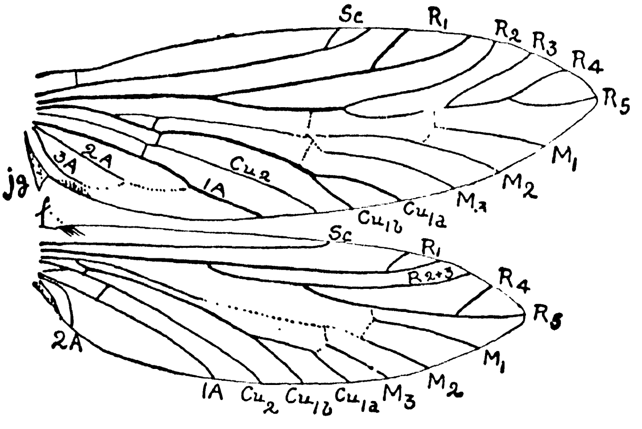

FIG. 425.—VENATION OF HOMONEURA (*MNEMONICA SUBPURPURELLA*).

jg, jugum; *f*, frenulum. Adapted from Tillyard. *Proc. Linn. Soc. N.S.W.* 44, pt. 1.

Among the Heteroneura there is a marked divergence in the venation of the two pairs of wings, but no annectent type has yet been discovered which serves to connect the most primitive forms with their homoneurous ancestors (Fig. 426). The most ancient type of venation is found among the Cossidæ (Turner) which, however, exhibits the characteristic heteroneurous features in the hind-wing, viz :—the fusion of Sc and R_1, the reduction of Rs, and the coalescence of 1A and 2A. As we ascend the lepidopterous series the vein Cu_2 disappears from both pairs of wings.

The *wing-coupling apparatus* attains a high degree of specialization among various Lepidoptera (Griffiths, 1898; Tillyard, 1918). Among Homoneura two distinct types are found, viz: the jugo-frenate and the jugate. The former method is found in the Micropterygidæ and the mechanism consists of both frenulum and jugum. The frenulum is usually composed of 3 or 4 bristles inserted on the costal border of the hind-wing. The jugum is present on the hind margin of the fore-wing but instead of passing backwards beneath the hind-wing, as is usually the case, it is folded forwards beneath the fore-wing. The frenulum becomes engaged in the space between the jugum and the lower membrane of the fore-wing and in this manner the two wings of a side are held together. In the Hepialidæ and Prototheoridæ the frenulum is wanting. The jugum is a finger-like process arising from the hind margin of the fore-wing near the base. It projects well beneath the costa of the hind-wing which becomes firmly held in the incision between the jugum and the hind margin of the fore-wing. Among Heteroneura two main types of wing-coupling apparatus are also evident, viz:—the *frenate* and the *amplexiform*. In the *frenate type* a sexual difference is very noticeable; thus in the male the frenulum consists of a single stout bristle which, however, can be clearly seen to be composed of several setæ fused together; in the female the bristles remain separate and vary from 2 to 9 in number. In strongly flying males the frenulum is often large and powerful, while among species in which the females are weak fliers or fly but little the frenulum is correspondingly reduced. In both sexes it arises from a small swelling at the humeral angle of the hind-wing, and passes beneath the fore-wing where its apex is retained in position by a locking mechanism or *retinaculum*, and in this manner the wings are held together. The retinaculum similarly exhibits sexual differences. In the female it is very simple, being nothing more than a group of somewhat stiffened hairs or scales arising in the neighbourhood of Cu_1. In the male it arises near the base of Sc and consists of a strong curved chitinous hook developed from the wall of that vein In *Synemon* (Castniidæ) both types of retinaculum are present in the male; the typically male hook-like organ is represented by the overlapping margin of a portion of Sc and is therefore less specialized than in other families. Tillyard, on the authority of Turner, states that this double type of retinaculum is widely spread among the males of many Lepidoptera. In many

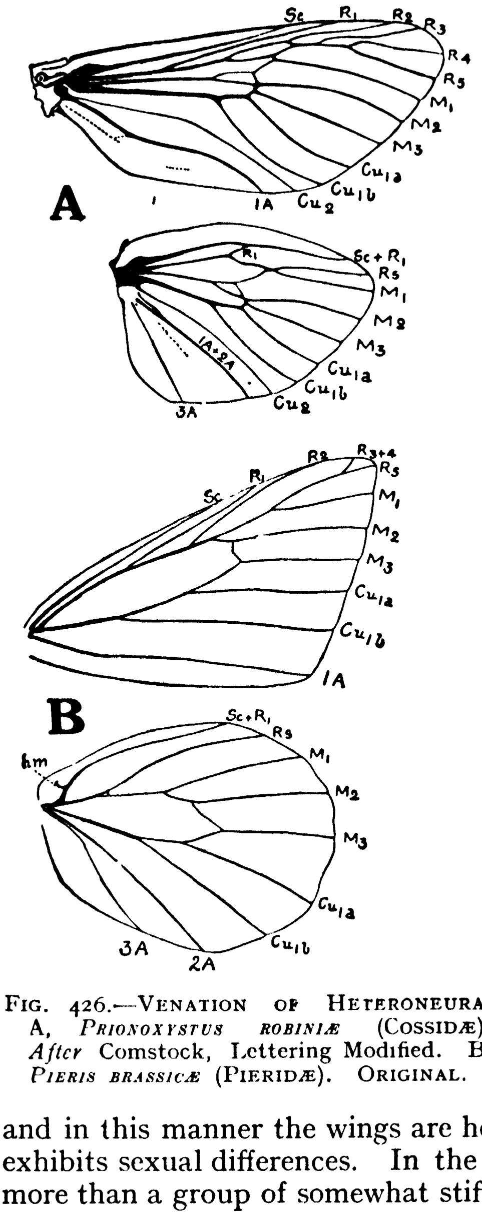

Fig. 426.—Venation of Heteroneura. A, *Prionoxystus robiniæ* (Cossidæ). *After* Comstock, Lettering Modified. B, *Pieris brassicæ* (Pieridæ). Original.

Sesiidæ, in which both sexes are swift fliers, the females exhibit the male type of frenulum and possess the hook-like retinaculum. In the *amplexiform type* the frenulum is lost, and the two wings of a side are maintained together owing to their overlapping to a very considerable degree. This condition is met with for example in the Saturniidæ, Lasiocampidæ, and in all the families of the Papilionina. The humeral lobe of the hind-wing is enlarged and often strengthened by the development of one or more short humeral veins, and projects far beneath the fore-wing. In the Castniidæ both the frenulum and humeral lobe are well developed, and from such a condition as this it is evident that the amplexiform type may have been derived through the loss of the frenulum. The course which necessitated the change is obscure but may perhaps be correlated with a change in the manner of flight. Intermediates between the above two types of wing-coupling apparatus are to be met with ; thus in *Bombyx mori,* the frenulum is vestigial and the humeral lobe well developed ; this same condition is found among other frenulum-losers such as the Lacosomidæ.

In the females of certain Geometridæ and Tineidæ and also those of the Psychidæ, *Orgyia,* etc., wings are either totally wanting, or reduced to small non-functional vestiges. This flightless condition evidently confines the females to a great extent to their larval food-plants and it is noteworthy that the latter are almost always very common and generally distributed species. The fact that the flightless females of the Geometridæ and Tineidæ belong to forms which occur during the colder months of the year has often been commented upon. This peculiarity has been explained as being an adaptation to prevent their leaving the food-plant and perishing owing to inclement weather. Some other explanation, however, needs to be formulated to account for the flightless condition of such eminently summer insects as *Orgyia* and the Psychidæ. It appears not unlikely that the loss of wings may be a mutation and is not to be accounted for on teleological grounds.

The ABDOMEN consists of ten segments ; the 1st segment is reduced and its sternum wanting or wholly membranous, the 7th and 8th are sometimes slightly modified in relation to the genitalia and the 9th and 10th segments are greatly modified in the latter respect. On either side of the metathorax or the base of the abdomen in many Lepidoptera there is a complex organ, the *tympanum.* This structure is well seen in the Geometridæ and appears as a bladder-like vesicle closely associated with the 1st abdominal spiracle of its side and certain of the neighbouring tracheal air-sacs. It is innervated from the last thoracic ganglion and, from its general structure, is presumed to be an auditory organ (Eggers, 1919 : see also p. 94).

The morphology and nomenclature of the male genitalia have become much involved but the work of Zander has contributed towards a better understanding of the subject (Fig. 427). The 9th segment or *tegumen* is a narrow ring encircling the apex of the body and its sternal region or *vinculum* is invaginated to form a median *saccus* which extends into the preceding segment. A pair of *claspers* or valves (harpes of Pierce, harpogones of White) are hinged to the *vinculum* and form the most prominent organs of the external genitalia. The *harpes* are spine-like structures often present in the inner aspect of the claspers. Attached to the hind margin of the 9th tergum is a median process or *uncus* which is usually hook-like or bifid, and in many Lepidoptera there is a median ventral sclerite or *gnathos* lying a short distance below it. The uncus and the gnathos have usually been regarded as the tergum and sternum of the 10th segment, but according to Zander they are secondary processes, the segment itself remaining membranous. The anus opens just beneath the uncus and between that sclerite and the gnathos. The *ædeagus* is situated below the gnathos and is enclosed in a sheath and at the point where the latter joins the body there is a sclerotized support or *juxta* (penis-funnel or ring-wall). For further information on the male genitalia reference should be made to the writings of Zander (1903), Pierce (1909–22) and Mehta (*Quart. Journ. Mic. Sci.* 76, 1933). In the female the terminal segments of the abdomen are sometimes attenuated and telescoped, thus functioning as a retractile ovipositor. An exserted sclerotized ovipositor is rarely present (vide Wood, *Ent. Month. Mag.* 189).

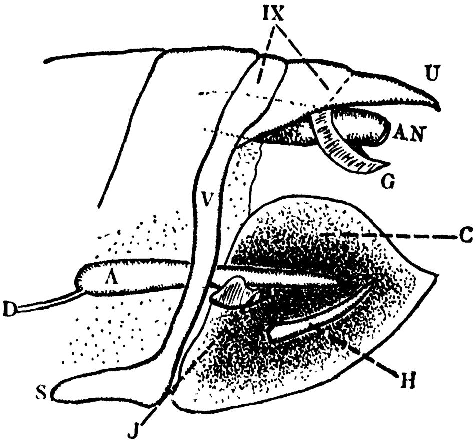

FIG. 427.—DIAGRAM OF MALE GENITALIA: LEFT SIDE REMOVED.

A, ædeagus; AN, anus; C, clasper; D, ejaculatory duct; G, gnathos; H, harpes; J, juxta; S, saccus; U, uncus; V, vinculum; IX, 9th segment (tegumen).

Internal Anatomy

The DIGESTIVE SYSTEM.—The cavity of the proboscis communicates with the pharynx and we owe to Burgess (1880) an account of the structure of the latter organ in *Danais*. It is an ovoid chamber provided with powerful muscular walls and issuing from between the fibres of the latter are five radial muscles, which pass outwards to be attached to the head capsule. When the latter muscles contract the pharyngeal cavity enlarges and a partial vacuum is created; this becomes filled by an ascent of fluid through the proboscis. The walls of the pharynx then contract, thereby forcing the food backwards into the œsophagus, and the closure of a pharyngeal valve precludes the return flow down the proboscis. The œsophagus is a long tube of very narrow calibre and, in the more primitive forms, expands distally into a well-developed crop (Homoneura, Cossidæ, Psychidæ, many Tineina, *Attacus*, *Phigalia*). In other species the crop takes the form of a lateral dilatation connected with the œsophagus by means of a wide-mouthed channel (*Adela* and other Tineina, Zygænidæ, certain Saturniidæ, *Ematurga*, etc.). In the majority of Lepidoptera the crop forms a large food reservoir connected with the fore-intestine by a short narrow duct. The stomach is a straight tube of relatively small capacity, and the hind-intestine consists of a narrow coiled ileum, a distended chamber or colon, and a short muscular rectum. Salivary glands take the form of a long coiled filamentous tube on either side, the silk glands of the larva degenerating in the pupa and being no longer evident. The Malpighian tubes are six in number, three of a side opening by a common duct into the commencement of the ileum. Exceptions are found in certain Tineina (*Tinea pellionella* and *T. bisselliella* and *Blabophanes rusticella*) which possess only a single pair, and in *Galleria mellonella* there are similarly two vessels but each is irregularly ramified (vide Cholodkovsky, 1887).

The NERVOUS SYSTEM (vide Newport, 1834; Brandt, 1879; Peterson, 1899; Buxton, 1917) exhibits a certain amount of concentration with regard to the ganglia of the ventral nerve cord. The most primitive condition is found in *Hepialus* in which there are three thoracic and five abdominal ganglia. In the *Micropterygidæ* and also *Tinea pellionella, Cossus, Sesia, Zygæna, Phalera* and *Ematurga* the 4th and 5th abdominal ganglia are fused into a large common centre. The majority of Lepidoptera, however, are characterized by two thoracic and four abdominal ganglia; those of the meso- and meta-thorax are fused and the abdominal ganglia lie in the 2nd to 6th segments. The Psychidæ are primitive but variable: thus Petersen records three thoracic and six abdominal ganglia in the female *Psyche unicolor* Hfm., while in *Fumea intermedia* and other species there are four abdominal ganglia in both sexes.

The DORSAL VESSEL has been very little investigated: Newport states that in most Lepidoptera there are eight pairs of lateral ostia, and in *Danais* Burgess states that slight constrictions divide the heart into a number of segments corresponding to those of the abdomen. In *Protoparce*, as Brocher has pointed out, the aorta makes a sharp loop in the thorax and at the apex of the bend it is connected with a pulsatile organ. This condition is probably general but it needs further research.

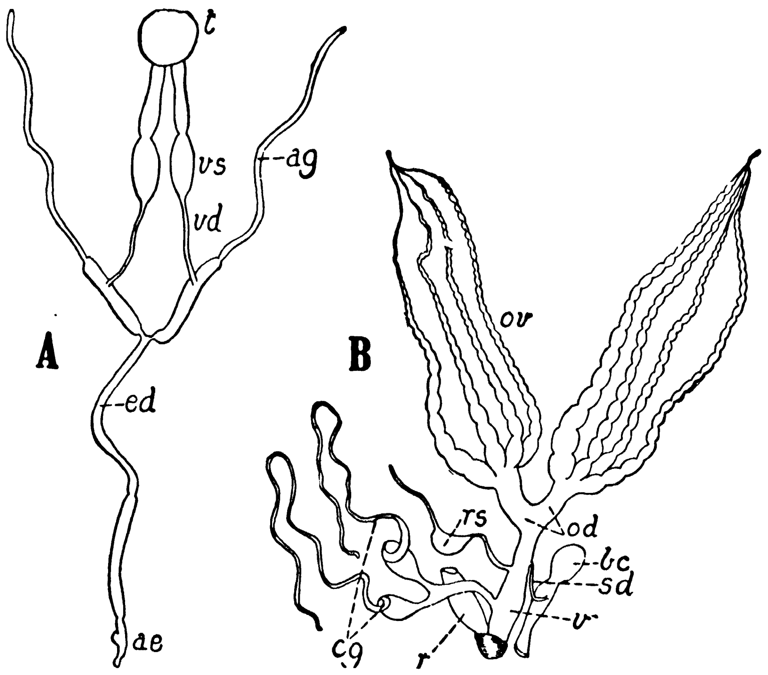

FIG. 428.—REPRODUCTIVE ORGANS OF *SMERINTHUS POPULI*.

A, MALE: *ae*, ædeagus; *ag*, accessory gland; *ed*, ejaculatory duct; *t*, testis; *vd*, vas deferens; *vs*, vesicula seminalis. B, FEMALE: *bc*, bursa copulatrix; *cg*, colleterial gland; *od*, oviduct; *ov*, ovary; *r*, rectum; *rs*, receptaculum seminis; *sd*, seminal duct; *v*, vagina.

The MALE REPRODUCTIVE ORGANS (Fig. 428, A) have been studied by Cholodkovsky (1884) in many species, and also by Stitz (1900), Petersen (1899) and Ruckes (1919). Typically each testes consists of four follicles exhibiting varying degrees of coalescence while among the higher Lepidoptera the two organs are intimately fused into a single median gonad. *Nematois* is exceptional in that each gonad consists of twenty follicles. Two principal types of reproductive system are distinguishable (1).—The testes are paired and each is enclosed in a separate scrotum. In *Hepialus* the follicles are separate and the gonad presents a digitate appearance: this condition is evidently the most primitive found in the order. In other cases the follicles are compressed together and surrounded by a common scrotum. This type is met with in the Micropterygidæ, certain Saturniidæ, *Bombyx mori, Lycæna arion, Parnassius* and a few others. (2).—The testes are fused and enclosed in a common scrotum: in some cases the paired nature of the gonad is still evident while in others the fusion is complete. This type (no. 2) is the prevalent one, and usually the follicles are spirally wound around the longitudinal axis of the gonad. The organs in *Samia cecropia* L. have been studied by Ruckes and in *Bombyx mori* by Verson. The testes lie in a dorso-lateral position, close to the alimentary canal and just beneath the 5th and 6th abdominal terga. The vasa deferentia are narrow tubes which enlarge proximally to form the vesiculæ seminales. Each receives a long filamentous accessory gland but, according to Ruckes, the structure of the latter is not markedly glandular, its walls being provided with longitudinal muscle fibres and it appears probable that the gland serves, along with the vesiculæ seminales, as a receptacle for storing the spermatozoa. The vesiculæ seminales unite to form a common ductus ejaculatorius which terminates in a bulbus ejaculatorius at the base of the ædeagus.

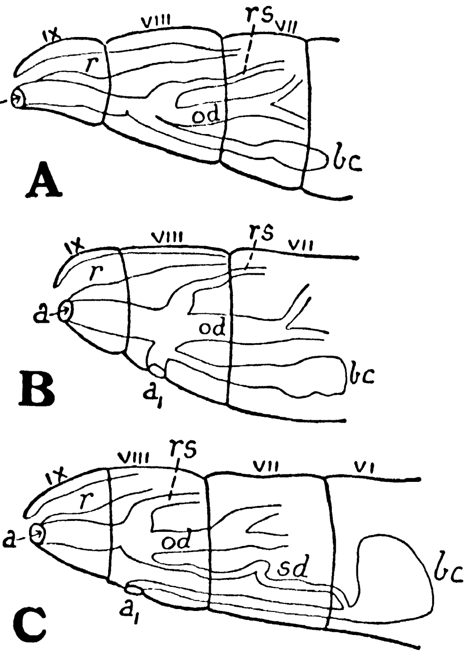

FIG. 429.—DIAGRAM OF THE MORPHOLOGY OF THE FEMALE REPRODUCTIVE SYSTEM IN A, MICROPTERYGIDÆ, ETC.; B, *PSYCHIDÆ*; C, *HETEROGENEA*, *CHEIMATOBIA*, ETC.

a, aperture of oviduct; a_1, aperture of bursa; *VI-IX*, 6th to 9th abdominal segments. Other lettering as in Fig. 414. *After* Petersen, 1899.

The FEMALE REPRODUCTIVE ORGANS (Fig. 428, B). Each ovary consists typically of four polytrophic ovarioles but a certain number of exceptions to this rule are known among the lower members of the order. Thus, there are six ovarioles to each ovary in *Psyche helix*, 10 to 12 in *Adela*, 14 in *Sesia scoliæformis*, and 12 to 20 in *Nematois*. Two principal types of reproductive system are prevalent (Fig. 429). In the primitive type (*Hepialidæ Micropteryx*, *Adela*, *Nepticula*, *Incurvaria*, certain Psychidæ, etc.) there is a single genital aperture on the 9th abdominal sternum which communicates with a median vestibule. The latter chamber is the terminal portion of the common oviduct, and receives the duct of the receptaculum seminis dorsally, and that of the bursa copulatrix ventrally. In the more specialized, and generally prevalent type, there are two reproductive apertures, viz.—an aperture opening on to the 8th sternum which is that of the bursa copulatrix, and the aperture of the common oviduct situated on the 9th sternum. The separation of the bursa copulatrix from the rest of the genital system is exhibited in the least modified condition in certain of the Psychidæ. In these instances the canal of the bursa copulatrix communicates with the common oviduct by an extremely short tube which is little more than an aperture in their intervening walls. In other Lepidoptera a definite canal or *ductus seminalis* is evident, and in the highest forms it is considerably lengthened and of exceedingly narrow calibre.

A pair of ramified or filiform colleterial glands open into bladder-like ducts which communicate with the common oviduct just behind the aperture of the receptaculum seminis. In many species (*B. mori*, etc.) an accessory gland is also present in relation with the latter structure, and the whole organ then resembles a colleterial gland in general appearance, and has often been referred to as such. We owe to Hatchett Jackson (1890) the first elucidation of the morphology and development of the female genital system in Lepidoptera. The bursa copulatrix is a secondary invagination of the ectoderm, but its aperture corresponds with the vaginal aperture in other orders. The opening of the common oviduct, on the other hand, has migrated backwards and taken up a secondary position on the 9th sternum. According to Balbiani (*Comp. Rend.* 1869) the bursa copulatrix receives the spermatozoa during copulation. Owing to the absence of muscles in the walls of that chamber, the spermatozoa migrate by their own motility into the ductus seminalis. They subsequently enter the oviduct and then pass up the duct leading into the receptaculum seminis, and are stored in the latter organ until the eggs enter the oviduct for fertilization. For detailed information on the female genital system reference should be made to the works of Eidmann (1929), Petersen (1899, 1904) and Stitz (1901).

The TRACHEAL SYSTEM communicates with the exterior by means of usually nine pairs of spiracles, two being thoracic and the remainder abdominal in position : the pair on the 8th segment of the abdomen, although present in the larva, is aborted.

The general LITERATURE dealing with the morphology of adult Lepidoptera is relatively small. The principal anatomical treatise is that of Petersen (1899) and a good deal of information on the external structure will be found in Rothschild and Jordan's monograph (1903). The most completely investigated species is *Bombyx mori* whose anatomy has been studied by many workers including Blanc, Verson, Tichomirov and others . for the general structure of *Danais*, vide Burgess (1880), while Brandt has dealt with that of *Hepialus* (1880) and the Sesiidæ (1890), and Nigmann (1908) with *Acentropus.*

CLASSIFICATION

The familiar division of the Lepidoptera into Rhopalocera (butterflies) and Heterocera (moths) has little to recommend it other than convenience founded upon usage. The main objection to its adoption is that the Rhopalocera, although they are of no higher rank than a superfamily, are elevated to a sub-order of equivalent value to the whole of the rest of the Lepidoptera. Again, the old divisions of Macro- and Micro-lepidoptera were founded mainly upon the size criterion. The adoption of these two groups led to the inclusion of certain families among the Macro-lepidoptera, whereas their true affinities lay with the division which comprised the " micros " in a literal sense. Nevertheless, after making the necessary adjustments in this respect, the retention of these two expressions does admit of certain convenience of reference, although they do not represent definable natural groups. As generally understood, the " Microlepidoptera " are the Homoneura and the sections Tortricoidea, Pyralidoidea and Tineoidea of the Heteroneura in the present work. Chapman (1893) gave a tentative grouping of the Heterocera based upon important pupal characters and suggested the divisions Obtectæ and Incompletæ (vide p. 430). About the same time Comstock brought forward a classification founded upon the venation and wing-coupling apparatus. He recognized two suborders, the Jugatæ and Frenatæ—the former possessing a jugum and the latter a frenulum. The presence of a frenulum, however, is too variable even within the limits of a single family to have very much classificatory value. In 1895 Packard laid stress upon Walter's researches on the mouth-parts and separated the order into the Lepidoptera Laciniata (or Protolepidoptera) and the Lepidoptera Haustellata, the main feature being the presence of biting mouth-parts in the former sub-order (which includes *Micropteryx*) and their absence in all other Lepidoptera. The Haustellata he further divided into the Palæolepidoptera (which includes the Eriocraninæ) and the Neolepidoptera. The latter he divided into two sections corresponding in the main to the Pupæ Incompletæ and Pupæ Obtectæ of Chapman. In the same year Meyrick brought out a classification based upon the venation in conjunction with other features and in 1895 Hampson published a revision of his earlier scheme (1892) also founded upon the venation. In addition to the above-mentioned systems, the eggs have been examined by Chapman (1896) and Tutt (1899), while classifications based upon larval characters have been advanced by Dyar (1894), Forbes (1910), Fracker (1915) and others: Mosher (1916) has re-examined the pupa from the same standpoint. Although no scheme based upon a single series of characters selected from one stage in the life-history can be regarded as anything approaching the ideal one, the venation on account of its constancy, affords the best features to work upon. For the primary division into sub-orders those suggested by Tillyard (1918) have been adopted. His sub-order Homoneura includes Meyrick's division Micropterygina and his Heteroneura the remainder of the order. The separation of the numerous families of the latter into major groups is extremely difficult as is witnessed by the lack of general agreement in the recent systems put forward in the works of Meyrick, Schröeder, Forbes and Tillyard. The classification given in the pages which follow attempts to take into account the importance of the tympanal organs combined with venational and other features while the family keys are mainly after Hampson. The larval and pupal characters are chiefly based upon those given by Fracker (1915) and Mosher (1916) respectively.

Key to the major groups of Lepidoptera.

1 (2).—Venation of fore- and hind-wings almost identical. **Homoneura.** (p. 444)
2 (1).—Venation of fore- and hind-wings with evident differences. **Heteroneura** (p. 446)
3 (18).—Hind-wings with Cu$_2$ absent.
4 (5).—Antennæ clavate, no frenulum. PAPILIONOIDEA (p. 461)
5 (4).—Antennæ acuminate or, if clavate a frenulum present.
6 (7).—Wings very narrow, venation degenerate. TINEOIDEA (part) (p. 447)
7 (6).—Venation well developed.
8 (11).—Wings cleft into plumes.
9 (10).—Plumes at most 4 to each wing. PYRALOIDEA (part) (p. 454)
10 (9).—Plumes more than 4 to each wing. TINEOIDEA (part) (p. 450)
11 (8).—Wings entire.
12 (15).—Tympanal organs present: frenulum present, rarely atrophied.
13 (14).—Tympanal organs in metathorax: fore-wing with M$_2$ usually basally approximated to M$_3$. NOCTUOIDEA (p. 470)
14 (13).—Tympanal organs in base of abdomen: fore-wing with M$_2$ rarely basally approximated to M$_3$. GEOMETROIDEA (p. 467)
15 (12).—Tympanal organs absent: frenulum often absent.

16 (17).—Antennæ gradually clubbed with apex pointed and usually hooked. Frenulum almost always strongly developed. SPHINGOIDEA (p. 469)
17 (16).—Antennæ pectinate or rarely simple: frenulum nearly always lost. BOMBYCOIDEA (p. 457)
18 (3).—Cu_2 present in hind-wing.[1]
19 (22).—In both wings stem of M present in cell: Cu_2 present in fore-wing.[2] Proboscis usually atrophied.
20 (21).—M forked in the cell: areole present. COSSOIDEA (p. 446)
21 (20).—M rarely forked in the cell: areole absent.[3] PSYCHOIDEA (p. 454)
22 (19).—Stem of M rarely present in the cell: Cu_2 wanting or vestigial in fore-wing. Proboscis usually present.
23 (24).—Hind wing with $Sc + R_1$ approximated to, or fused with, Rs beyond the cell then diverging. Tympanal organs present.[4] PYRALOIDEA (part) (p. 452)
24 (23).—Hind-wing with $Sc + R_1$ remote from Rs beyond the cell: no tympanal organs.
25 (26).—3rd segment of labial palp short, usually obtuse: in hind-wing M_1 and Rs usually approximated or stalked. TORTRICOIDEA (p. 451)
26 (25).—3rd segment of labial palp slender and pointed: in hind-wing M_1 and Rs separate, less often approximated or stalked. TINEOIDEA (part) (p. 447)

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[1] Absent or vestigial in Thyrididæ, a few Castniidæ and in some Tortricoidea.
[2] Absent in Teragridæ. [3] Except in some Castniidæ. [4] Absent in Thyrididæ.

Sub-Order HOMONEURA

VENATION OF FORE- AND HIND-WINGS ALMOST IDENTICAL. IN BOTH PAIRS OF WINGS RS IS 3- OR 4-BRANCHED. A SPIRAL PROBOSCIS IS NEVER DEVELOPED.

FAM. MICROPTERYGIDÆ. MOUTH-PARTS WELL DEVELOPED, TIBIAL SPURS PRESENT, WING-COUPLING APPARATUS OF JUGO-FRENATE TYPE CONSISTING OF JUGAL LOBE, HUMERAL LOBE AND FRENULUM. This family is of great importance from the standpoint of phylogeny as it includes the most primitive of all Lepidoptera. They are small diurnal moths with a wing-expanse sometimes less than 7 mm., and rarely exceeding 15 mm. The fore-wings are ovate-lanceolate with metallic colouring. Like many ancient groups, they enjoy an extremely wide distribution, but the family has probably yet to be identified in many parts of the world. Well known British genera are *Micropteryx* Hb. (*Eriocephala* Curt.) and *Eriocrania* Zel. (*Micropteryx* aut.); *M. calthella* L. is a common insect during late spring in many parts of the British

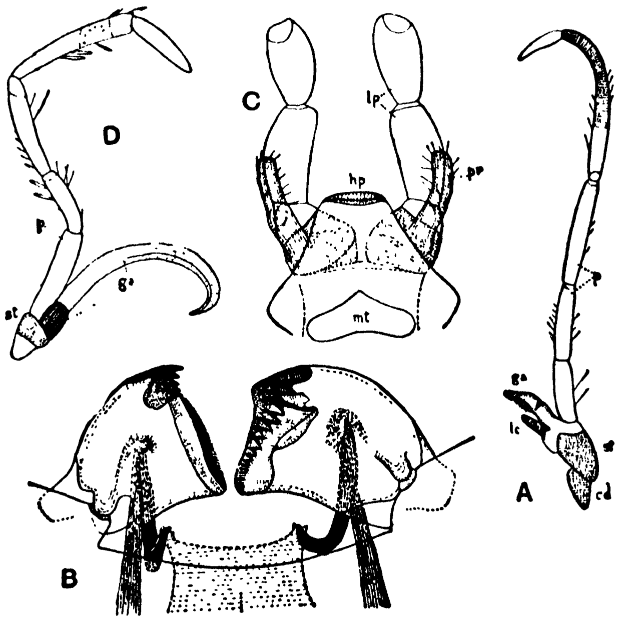

Fig. 430.—Mouth-parts of Micropterygidæ. A, *Micropteryx*, 1st Maxilla. B, *Sabatinca*, Mandibles. *C*, *Sabatinca*, Labium, oral aspect; *D*, *Eriocrania*, 1st Maxilla.

cd, cardo; *ga*, galea; *hp*, hypopharynx; *lc*, lacinia; *lp*, labial palp; *mt*, mentum; *p*, maxillary palp; *pr*, process of labial palp; *st*, stipes. *After* figures by Tillyard, *Trans. Ent. Soc.* 1923.

Isles. The New Zealand genus *Sabatinca* Walk. exhibits the most primitive venation, which is almost identical with that of the Trichopteron *Rhyacophila.*

The sub-family Micropteryginæ includes *Micropteryx, Sabatinca,* and two doubtful genera. Functional mandibles and laciniæ are present and the galeæ are free (Fig. 430), there being no proboscis. As in all members of the family the ligula is atrophied and the labial palpi are 3-jointed organs. These insects are pollen feeders and use their maxillæ for the purpose. The larva of *Micropteryx* occurs in wet moss and is characterized by the presence of eight pairs of abdominal limbs (vide Chapman, *Trans. Ent. Soc.,* 1894). These appendages closely resemble the thoracic legs in being jointed and each is terminated by a claw. The body bears eight rows of metamerically arranged globose processes. The larva of *Sabatinca* (Tillyard, 1922) lives among liverworts and has a similar number of reduced abdominal limbs: the pupa is characterized by the possession of functional mandibles.

The Eriocraniinæ have lost the laciniæ and the galeæ are adapted to form a short proboscis. Mandibles are frequently erroneously stated to be absent: they are reduced though distinct, and are non-denticulate (Walter, 1885). They are visible within the bases of the pupal mandibles and possess strongly developed abductor and adductor muscles identical with those of the pupa (Busck and Boving). The larvæ of *Eriocrania* are apodous leaf-miners in birch, hazel, oak, and chestnut: the head is very small and partly hidden by the large prothorax and the usual number of spiracles are present. Pupation takes place in a tough cocoon of silk and earthen particles and the pupa closely resembles that of a Trichopteron. It is of the typical exarate type, with the appendages free and the abdominal segments moveable. The most conspicuous organs are the long curved serrated mandibles which are used to rupture the cocoon and aid the pupa in making its way to the surface of the soil. For the metamorphosis and detailed structure of all stages of *Mnemonica,* vide Busck and Boving (1914); and for the pupa of *Eriocrania,* vide Chapman (1893A).

The Mnesarchæiinæ include the most specialized members of the family and are represented by the New Zealand genus *Mnesarchæa.* Mandibles are wanting, the maxillary palpi are 3-jointed only, laciniæ are absent and the galeæ form a rudimentary proboscis used as a sucking-organ. Their metamorphoses are unknown.

Much difference of opinion has been expressed with regard to the systematic position of the Micropterygidæ, and their affinities are fully discussed by Tillyard (1919). Both the latter observer and Meyrick regard these insects as being true Lepidoptera, Comstock considers that they are terrestrial Trichoptera while Chapman (1917) takes the extreme step of separating the genus *Micropteryx* into an independent order—the Zeugloptera. Tillyard enumerates four salient differences between this family and the Trichoptera, viz. M_4 is not present as a separate vein in the fore-wing whereas it exists in archaic Trichoptera; the pupal wing-tracheation is complete whereas in Trichoptera it is reduced to two tracheæ only; the characteristic Trichopterous wing-spot is absent: and broad scales with numerous striæ are present, whereas scales only appear in a few isolated and highly specialized Trichoptera, and then only of narrow primitive form with few striæ.

FAM. HEPIALIDÆ (Swift-Moths). ANTENNÆ VERY SHORT, MOUTH-PARTS VESTIGIAL. WING-COUPLING APPARATUS OF JUGATE TYPE, THE JUGAL LOBE ELONGATE AND USUALLY PASSING BENEATH THE HIND-WING. TIBIAL SPURS ABSENT. A family comprising about 200 species which are widely distributed but best represented in Australia. It is a peculiarly isolated group and although primitive in many features of the external and internal anatomy it is specialized in certain others. The species are extremely rapid fliers and vary greatly in size: some are relatively gigantic, attaining a wing expanse of about 180 mm. Although the five British representatives are sombre-coloured insects certain of the great Australian and S. African forms (*Charagia, Leto*) are magnificently decorated with green and rose or adorned with metallic markings. The European species are crepuscular, or fly before dusk, and in two cases at least the mating habits are exceptional in that the female seeks the male. In *Hepialus humuli* the male is commonly white and is readily sought out by the female: in *H. hectus* the female discovers the male by means of an odour diffused by the latter. The larvæ are subterranean, feeding upon roots, or are internal wood feeders. Those of several European species are described by Fracker (1915), and Quail (*Trans. Ent. Soc.,* 1900) has contributed observations on the metamorphoses of certain Australian forms. They are elongate, devoid of colour pattern and both tufted and secondary setæ are wanting. The crochets are disposed in a complete multiserial circle. The pupæ are unusually elongate and active and are armed with spines, toothed ridges, and cutting plates on the abdominal segments, which are special adaptations for making their way to the surface. The 2nd to 6th abdominal segments are free in the female, and the 7th also in the male. For a discussion of the early stages and affinities of the family, vide Packard (1895).

The small family Prototheoridæ from S. Africa is related to the Hepialidæ. The Australian family Palæosetidæ is imperfectly known but is also related to the Hepialidæ.

Sub-Order HETERONEURA

VENATION OF FORE- AND HIND-WINGS MARKEDLY DIFFERENT: HIND-WINGS WITH RS REDUCED TO A SINGLE VEIN. A SPIRAL PROBOSCIS PRESENT EXCEPT IN GROUPS WHERE IT HAS ATROPHIED.

Superfamily Cossoidea (Figs. 426, 431).

BOTH PAIRS OF WINGS WITH CU_2 PRESENT AND M FURCATE WITHIN THE CELL. AREOLE PRESENT IN FORE-WING. HAUSTELLUM ABSENT.

FAM. COSSIDÆ (Goat Moths, Carpenter Moths).—Insects of moderately large or exceedingly large size, the females of *Duomitus leuconotus* Wlk. attaining a wing-expanse of 180 mm. The family is generally distributed and, according to Turner (1918), it retains the most ancient form of venation among Heteroneura. The antennæ are frequently bipectinate in both sexes, rarely simple: in other cases they are bipectinate in the male for a portion of their length and filiform distally. The frenulum is sometimes short and apparently non-functional, more often it is well developed: in the female it may consist of as many as nine bristles (Hampson). These moths are nocturnal fliers and lay their eggs on the bark of trees, or in the tunnels from which they have emerged. The larvæ are internal feeders boring large galleries in the wood of forest, shade, and fruit trees or in the pith of reeds, etc., often causing serious injury. The head is closely united to the enlarged prothorax, and the mandibles are very large. Only primary setæ are present and the full number of limbs is retained, the crochets being usually either bi- or tri-ordinal, arranged in a complete circle. In certain species the larvæ attain a very large size and in *Cossus cossus* L. (*ligniperda* F.) and *Prionoxystus robiniæ* they live for at least two years. The pupæ lack maxillary palpi: the 3rd to 6th abdominal segments are moveable in the female and the 7th also in the male. The dorsum of the segments is armed with a toothed ridge along each margin and a cocoon of silk and gnawed wood is usually constructed. *Cossus* L. is one of the most primitive genera and is universally distributed. *Xyleutes* Hubn. includes numerous species found in all warmer regions, particularly Australia. *Zeuzera* Latr. includes the Leopard moth (*Z. pyrina* L.) whose larva is destructive to the wood of fruit trees (Fig. 431): that of *Z. coffeæ* Nietn. is known as the "White Borer" of coffee.

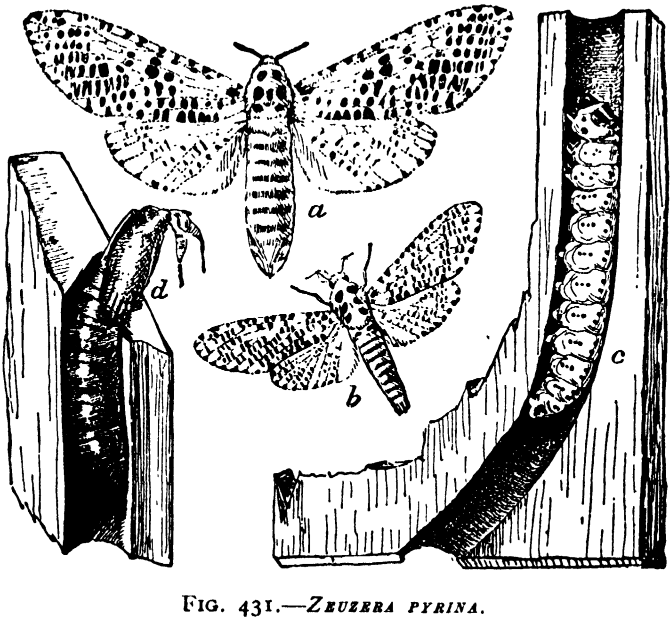

FIG. 431.—*ZEUZERA PYRINA.*

a, female; *b*, male; *c*, larva; *d*, pupal case. Actual size. *After* Howard and Chittenden. *U.S. Dept. Agric. Circ.* 109 (reduced).

Superfamily Tineoidea (Figs. 432, 433).

MAXILLARY PALPI OFTEN FULLY DEVELOPED: LABIAL PALPI WITH 3RD SEGMENT USUALLY SLENDER AND POINTED. CU_2 GENERALLY PRESENT IN BOTH WINGS BUT OFTEN REDUCED IN FORE-WING. HIND-WING WITH $SC + R_1$ FREE, LESS OFTEN JOINED TO CELL BY A BAR. M_1 AND RS SEPARATE, SOMETIMES APPROXIMATED OR STALKED: OR, VENATION DEGENERATE IN MANY SMALL SPECIES: OR, WINGS DIVIDED INTO PLUMES.

Table of groups.

1 (4).—Wings entire.	
2 (3).—$Sc + R_1$ evident in hind-wing.	**Tineina** (p. 448)
3 (2).—$Sc + R_1$ apparently absent in hind-wing.	Sesiidæ (p. 447)
4 (1).—Wings divided into plumes.	Orneodidæ (p. 450)

FAM. SESIIDÆ (**Ægeriidæ**: Clear wings).—This family is distinguishable by $Sc + R_1$ in the hind-wings being concealed by a fold of the costa. Their most striking character, however, is the absence of scales from the greater part of both pairs of wings: the antennæ are often dilated or knobbed and the abdomen is terminated by a conspicuous fan-like tuft of scales. The fore-wings are extremely narrow owing to the great reduction of the anal area and in most species the bristles of the frenulum in the female are consolidated as in the male. The family is characteristic of the northern hemisphere, and the species are diurnal, flying rapidly during warm sunshine. Many resemble wasps, bees, ichneumons, etc., in appearance, which is largely due to their clear wings, slender bodies and often bright colours. They are in many ways an aberrant group, especially as regards the internal anatomy (vide Brandt, 1890). The larvæ feed in the wood of trees and bushes or in the root-stocks of plants. They are colourless with greatly reduced setæ; the abdominal feet bear two transverse bands of uniordinal crochets, and a single row on the anal claspers. Among other characters Fracker states the spiracles of the 8th segment are much larger and higher up than on other abdominal segments. Pupation takes place in the larval gallery and the pupæ are provided with various forms of cutting plates for working their way to the surface: these are mostly situated on the head which is heavily chitinized. There are two rows of spines on most of the abdominal segments which extend around to the ventral surface, and a definite cremaster is wanting. Owing to

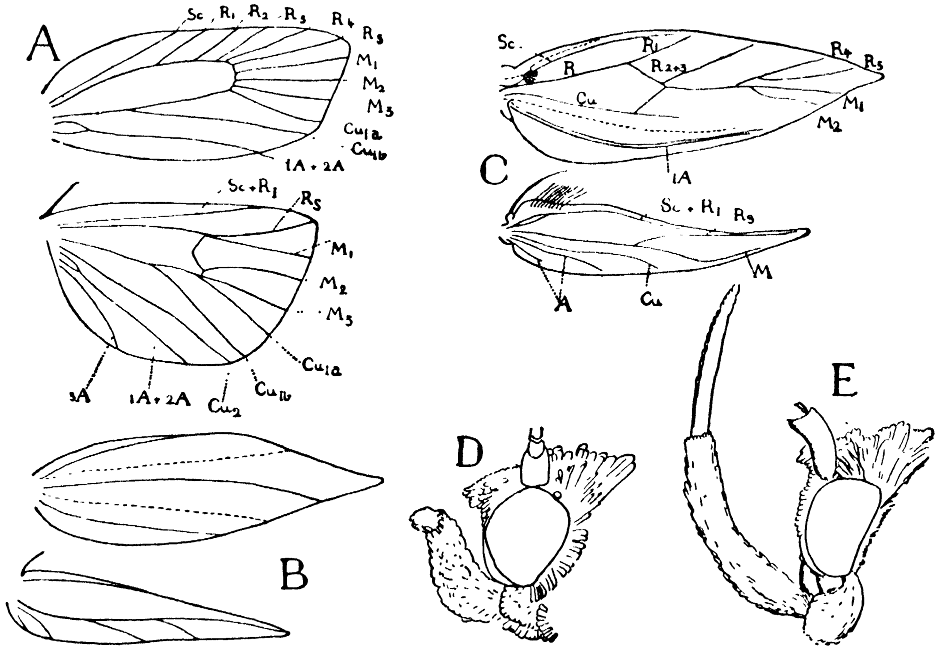

FIG. 432.—WINGS OF A, *PERONEA* (TORTRICIDÆ), B. *OPOSTEGA* (ADELIDÆ) AND C, *OBRUSSA* (NEPTICULIDÆ). D, SIDE VIEW OF HEAD SHOWING LABIAL PALP OF *CYDIA POMONELLA* (EUCOSMIDÆ): E, THE SAME OF *CRYPTOLECHIA TENTORIFERELLA* (ŒCOPHORIDÆ). Adapted from Meyrick (A, B), Braun (C) and Forbes (D, E).

their internal feeding habit several species have attracted the notice of economic entomologists, particularly the European and American Currant Borer (*Sesia tipuliformis*) and the Peach Tree Borer (*Sanninoidea exitiosa* Say) of the latter continent (vide *Bull.* 329 *Ohio Exp. Sta.*). Over 100 species of the family are palæarctic and no less than 90 belong to the genus *Sesia* : 15 species have been found in the British Isles but several are rare and local.

Tineina. The majority of the Tineoidea belong to this series, which includes about one-third of the Lepidoptera and over 750 species are British. Most of them are easily recognizable as narrow-winged insects bordered with long hair fringes: the larger and broader winged forms have shorter fringes and can usually be identified by the venational characters previously enumerated. The classification of the group presents great difficulties owing to the fact that notwithstanding the marked differences of the structure found in the extreme forms, the latter are closely interconnected by numerous gradational genera. The leading authorities are at variance as to the number of families that exist, and recent research has tended towards the recognition of an increasing number. Among this vast assemblage greater variation of larval habits and structure is found than in any other group of Lepidoptera.

FAM. GELECHIIDÆ.—Antennæ rarely with basal pecten. Fore-wings trapezoidal, posterior margin sinuate or emarginate. Hind-wings with Rs and M_1 stalked or approximated at base. This family includes nearly 400 genera and about 3,600 species of small moths represented nearly all over the world. A few forms have the hind-wings elongate-ovate and resemble Œcophoridæ, but may be separated from them by Rs and M_1 being basally approximated or stalked. The larvæ usually feed among spun leaves or shoots, sometimes in seedheads or roots, but are seldom leaf-miners or case-bearers (Meyrick). One of the best known species is the nearly cosmopolitan Angoumois Grain Moth (*Sitrotroga cerealella*), whose larvæ are destructive to wheat, maize, etc. The pink boll-worm (*Platyedra gossypiella*) is the widest spread and one of the most destructive of all cotton pests, few cotton regions being free from it. The potato tuber moth (*Phthorimæa operculella*) is a widespread pest of stored potatoes, more rarely affecting the field crop, and *Holcocera pulverea* is an important enemy of lac in India, its larvæ being predaceous on the latter insect. Over 130 species of the family are British.

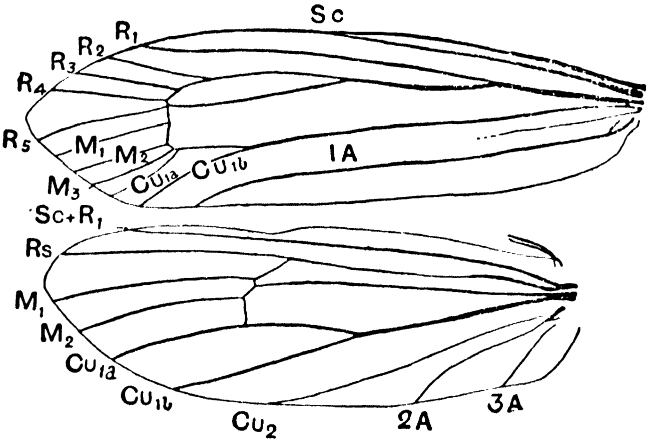

FIG. 433.—*HYPONOMEUTA EUONYMELLA*, LEFT WINGS. × 15.

FAM. COSMOPTERYGIDÆ.—Antennæ with a slight basal pecten. Fore-wings lanceolate or linear : hind-wings as in Gelechiidæ. A neglected but widely distributed group of about 1,000 species of small narrow-winged moths, of which 27 are British. The larvæ have varied habits, usually fixed for a genus : many are leaf-miners, some feed in shoots or seeds, others among dry refuse or attack scale-insects. The species of *Cosmopyteryx* are elegantly marked with black, orange and gold and the larvæ usually form blotch mines in leaves.

FAM. ŒCOPHORIDÆ.—Antennæ usually with a basal pecten. Hind-wings with Rs and M separate and parallel. A family comprising nearly 300 species, nearly half of which are Australian : 19 genera and 75 species are British. The larvæ feed among spun leaves or seeds, in decaying wood, etc. In the large genus *Depressaria* the larvæ affect more especially Compositæ and Umbelliferæ : the common *D. heracliana* spins together the flower heads and seeds of the parsnip and other plants in Europe and N. America. *Blastobasis* and its allies are often regarded as a separate family : their larvæ feed on dry refuse, seeds, etc., or live as parasites of scale-insects.

FAM. XYLORYCTIDÆ.—Antennal pecten absent. Hind-wings with Rs and M_1 basally approximated or stalked. This family includes some of the largest Tineoidea, and is especially well represented in Australia with a smaller number of species in S. America, India, etc. Some of the finest species belong to the genera *Cryptophasa*, *Maroga, Uzucha* and *Xylorycta*: they are often conspicuously coloured and attain a wing-expanse up to about 3 inches. The larvæ are concealed in shelters or coverings, or tunnel in wood carrying leaves for food.

FAM. HYPONOMEUTIDÆ.—A family of about 800 species whose tropical representatives are often brightly coloured and of relatively large size. The small ermine moths (*Hyponomeuta*) are very widely distributed and their larvæ live gregariously on shrubs and fruit trees. The large genus *Argyresthia* is well represented in Europe and N. America, the larvæ living in shoots, leaf-buds, fruit, etc. The species of *Ethmia* are sometimes regarded as a separate family: the larvæ are partial to Boraginaceæ living in a slight web on the leaves.

FAM. ELACHISTIDÆ (CYCNODIIDÆ).—A restricted family whose most important genus is *Elachista*, with over 200 species. The larvæ mostly mine leaves, especially of grasses or allied orders of plants. Mention needs also to be made of the small families *Douglasiidæ*, *Heliozelidæ* and *Scythridæ*, which appear to belong here and are sometimes included as subfamilies.

FAM. COLEOPHORIDÆ.—In this small family the only extensive genus is *Coleophora*, which is represented by over 400 holarctic species: about 90 species occur in N. America and 79 species in Britain. They are narrow-winged insects, usually recognizable by the antennæ being held in a correct position in repose. With regard to the larval habits, Meyrick remarks that they are leaf-mining when very young, afterwards inhabiting a portable case. The latter is attached to a leaf or seed-vessel and the larva bores into the interior. In the case of leaves a pale blotch is usually produced, with a distinctive round hole in one membrane.

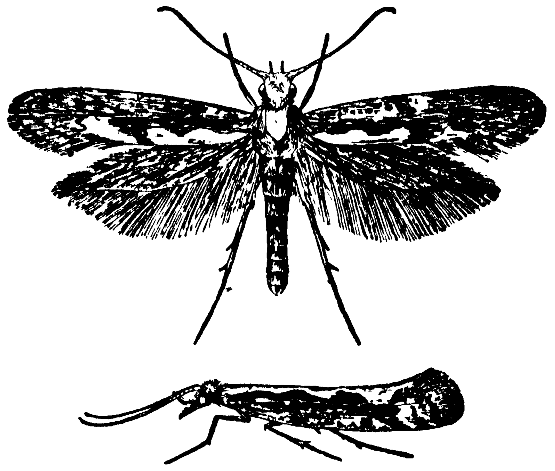

FIG. 434.—*PLUTELLA MACULIPENNIS*, ENLARGED.
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FAM. GRACILARIIDÆ.—A cosmopolitan family of about 1,000 small species with narrow, long-fringed wings. They are often recognizable by their habit of resting with the fore-part of the body upraised by the rather widely separated two anterior pairs of legs. The larvæ are leaf-miners: when young are very much flattened with blade-like mandibles and vestigial maxillæ and labium. At this stage they lacerate the cells and suck the exuding sap: later they usually undergo hypermetamorphosis, acquiring normal mouth-parts and devour the parenchyma. The mines in *Lithocolletis* are small blotches, of which one surface is silk-lined and caused to contract, thus producing a hollow chamber: the contracting surface may be either on the upper or lower leaf surface but is constant for a species (Meyrick). The two larger genera, *Lithocolletis* and *Gracilaria*, together include over 450 species: *Phyllocnistis*, with over 50 species, includes some of the smallest and most delicate of all moths, and is remarkable in that the larvæ are apodous.

FAM. PLUTELLIDÆ.—A family of about 200 species, occurring in most regions. They resemble the Hyponomeutidæ, but may be distinguished by the short porrect maxillary palpi. The larvæ feed in a slight web in leaves or occasionally mine leaves or stems: those of the cosmopolitan genus *Plutella* feed on the leaves of Cruciferæ. The diamond back moth (*Plutella maculipennis*: Fig. 434) is very destructive to vegetables and, owing to its ability to flourish in about all climates, it has become one of the most universally distributed of Lepidoptera and appears to be still extending its range through the agency of commerce. The small family *Epermeniidæ* is closely related to the Plutellidæ.

FAM. HELIODINIDÆ.—A moderate-sized cosmopolitan family, whose members when at rest have the trait of displaying the hind legs either upraised or applied to the back or sides of the body: the posterior legs have the tibiæ and tarsi furnished with whorls of bristles. An important genus is *Strathmopoda*, whose larvæ in some species prey upon Coccids, in others they bore into fruits, leaves, etc. Out of about 100 known species six are British.

FAM. GLYPHIPTERYGIDÆ.—A large family (about 800 spp., 12 British), especially abundant in the southern hemisphere. *Glyphipteryx* includes metallic-winged moths which fly in sunshine and whose larvæ feed chiefly on grasses and sedges. In *Choreutis* the moths resemble Tortrices in form and their larvæ often form webs among leaves or seeds.

FAM. TINEIDÆ.—A world-wide family of over 2,400 species characterized by the head being usually rough-haired, the proboscis short or absent and the maxillary palpi often long. The labial palpi are usually porrected and the posterior tibiæ hairy. The venation is very degenerate in some forms (*Opostega, Lyonetia*, etc., Fig. 432) which have the wings partially clothed with aculei and are often grouped into a separate family—the Lyonetiidæ. For the rest of the family the wings have all the veins present and separate, the hind pair being narrow. *Tinea* is universally distributed; its larvæ show diverse habits and sometimes live in portable cases. Those of most European species feed upon various dry animal or plant material. Thus, the larva of *T. vastella* feeds upon dried fruit, horns of antelopes, and other dried matter: those of *T. pellionella* and *biselliella* and *Trichophaga tapetiella* are "clothes moths"—household pests attacking clothing, carpets, furs, feathers, etc. In *Melasina energa* (Ceylon) Fryer states that the larva inhabits a tubular tunnel of earth and vegetable particles, which partly projects above the surface of the ground.

FAM. ADELIDÆ.—The species have the wing membrane closely covered with aculei and the venation well developed. In *Adela* and *Nemotois* the moths are often metallic and fly in sunshine. In the males, the antennæ are longer than in the females and often many times longer than the insect: the eyes in the males are often greatly enlarged and approximated dorsally. *Incurvaria* and its allies possess a strong cutting ovipositor for inserting the eggs into plant tissues. In the North American subfamily Prodoxinæ there is an intimate relationship between the moths and species of Yucca. The female *Tegeticula yuccasella* is associated with *Y. filamentosa* and by the aid of her specially modified mouth-parts collects the pollen and applies it to the pistil in which she has deposited an egg. In this way development of the fruit, upon which the larva feeds, is ensured. In *Prodoxus* the above relationship does not exist and the insect is dependent upon the *Tegeticula* for the pollination of the Yucca flowers, within which the larval growth similarly takes place.

FAM. NEPTICULIDÆ.—*Nepticula* and its allies include the smallest of the Lepidoptera, *N. microtheriella*, having a wing expanse of only 3 to 4 mm. The wings are clothed with aculei and are narrowly lanceolate, with a peculiar venation unlike that of all other Lepidoptera (Fig. 432). In certain species a jugum is present on the fore-wing in the female together with a row of hooked spines on the hind wing: in the male a true frenulum is present (Braun). The larvæ are mostly leaf-miners and are devoid of jointed legs or crochets: two pairs of leg-like swellings are present on the thorax and similar structures on the 2nd to 7th abdominal segments. *Nepticula* includes 67 British species, and is nearly world-wide in range.

Mention needs also to be made of four small families which are either largely or entirely Australasian. The **Epipyropidæ** have larvæ which are parasites upon Jassids and Fulgoroids. The **Cyclotornidæ** also include parasites: the 1st instar larvæ of the Australasian *Cyclotorna* parasitize Homoptera while, in their 2nd instar, they live in ants' nests (Dodd, *Trans. Ent. Soc.* 1912). The **Amphitheridæ** and **Copromorphidæ** each include a small number of species.

FAM. ORNEODIDÆ (Alucitidæ: Many Plume Moths).—A small isolated family characterized by both pairs of wings being cleft into six or more narrow plume-like divisions, densely fringed with hairs along both margins (Fig. 435). They are related to the Pyralids and Tineids, but exhibit no close affinity with the Pterophoridæ. With the exception of *Orneodes hexadactyla* L., which is European, the various species have a restricted range: the former insect is common in Britain, where it is the sole representative of the family. The larvæ burrow into shoots, flower-stalks, and buds giving rise to galls, and the known food-plants include *Lonicera, Scabiosa*, and *Stachys*. They are hirsute, cylindrical and rather stout; the crochets are uniordinal, arranged in a complete circle. The pupæ are very different from those of the Pterophoridæ and have affinities with Tineids and

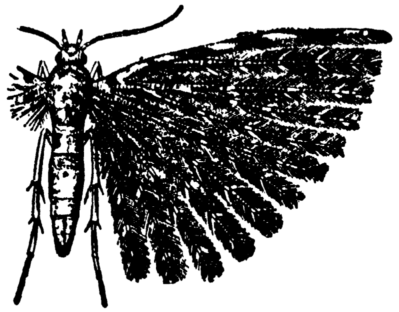

FIG. 435.—*ORNEODES PYGMÆA*, ENLARGED, CEYLON.
After Fletcher.

Pyralids. A cocoon is formed on the surface of the ground and consists of loose silk or of fine earthen particles. Most of what is known concerning the family will be found in papers by Chapman (1896), Hofmann (*Deut. Ent. Zeit.* 1898), Fletcher (*Spolia Zeyl.* 1910), and in *Genera Insectorum* by Meyrick (Fasc. 108).

Superfamily **Tortricoidea** (Tortrices: Fig. 432 A, D).

MAXILLARY PALPI VESTIGIAL OR ABSENT: LABIAL PALPI WITH 2ND SEGMENT MORE OR LESS ROUGH-SCALED, 3RD SEGMENT SHORT AND USUALLY OBTUSE. CU$_2$ GENERALLY PRESENT IN BOTH WINGS THOUGH OFTEN VESTIGIAL, ESPECIALLY IN FORE-WING. HIND-WING WITH SC + R$_1$ APPROXIMATED, OR LESS OFTEN JOINED, TO CELL THEN DIVERGING; M$_1$ AND RS USUALLY APPROXIMATED OR STALKED.

Table of families:

1 (4).	—Fore-wing with Cu$_{1b}$ arising from or near lower angle of cell.	
2 (3).	—Hind-wing with one or two branches to M.	Carposinidæ
3 (2).	—Hind-wing with three branches to M.	Phaloniidæ
4 (1).	—Fore-wing with Cu$_{1b}$ arising from near middle of cell.	
5 (6).	—Hind-wing with cubital pecten on margin of cell.	Eucosmidæ
6 (5).	—Hind-wing usually without cubital pecten.	
7 (8).	—Fore-wings with R$_3$ and R$_4$ stalked or coincident: end of palpus pointed.	Chlidanotidæ
8 (7).	—Fore-wings with R$_3$ and R$_4$ separate, if not end of palpus obtuse.	Tortricidæ

The Tortrices are moths of small size with wide wings, and the hair-fringes of the latter are always shorter than the width of the wing. The family is more characteristic of temperate regions than tropical, and the imagines are mainly crepuscular in habit. In the males of many species there is a basal costal fold to the fore-wings, often including expansible hairs, probably functioning as a scent organ. The eggs are flattened and oval, usually smooth, occasionally reticulated. The larvæ live concealed, usually in rolled or joined leaves, or in shoots spun together. Others live in stems, roots, flower-heads or seed-pods. They are rather elongate, slightly hairy and have the full number of abdominal limbs. The crochets on the abdominal feet are usually bi- or tri-ordinal, and arranged in a complete circle. The pupæ have two rows of spines on most of the abdominal segments; the 4th to 6th segments are movable in the female and the 7th also in the male. The pupa is protruded from the cocoon prior to the emergence of the imago and is usually found in the situation where the larvæ feed.

FAM. EUCOSMIDÆ (Olethreutidæ).—A family of over 2,000 species and including nearly two-thirds of the British Tortrices. *Laspeyresia*, with over 300 species, is widely distributed and its larvæ usually feed in fruits or stems. *L. molesta* is the Oriental Peach Moth which has become an established pest in N. America and S. Europe, probably from Japan. *Evetria* includes the destructive Pine-Shoot Moths and *Cydia* (*Carpocapsa*) *pomonella* is the Codling Moth, whose larva burrows in the fruit of the apple and is a world-wide enemy of the cultivator.

FAM. TORTRICIDÆ.—A family of about 1,500 species of world-wide range. In the large genus *Tortrix*, with some 300 species, *T. viridana* of Europe is a well-known defoliator of the oak: its economy and parasites have been studied by Silvestri (*Boll. Lab. Zool. Portici* 17, 1923). *Sparganothis* is exceptional in retaining the cubital pecten and *S. pilleriana* is a European pest of the grape. The larvæ of species of *Cacœcia* live in communal nests on trees and shrubs.

FAM. PHALONIIDÆ (Conchylidæ).—A family of mainly holarctic range, and whose larvæ are internal feeders, usually in flowers, seed-heads or stems. In *Phalonia* (over 220 species) the larvæ especially affect Compositæ. The **CARPOSINIDÆ** are a small family mainly found in Hawaii and Australasia and have Tineoid affinities, while the **CHLIDANOTIDÆ** are an Indo-Australian group.

Superfamily **Pyraloidea** (Fig. 436).

MAXILLARY PALPI USUALLY PRESENT. LEGS ALMOST ALWAYS LONG AND SLENDER. ABDOMINAL TYMPANAL ORGANS PRESENT IN MOST SPECIES. CU_2 VESTIGIAL OR ABSENT IN FORE-WING, ALMOST ALWAYS PRESENT IN HIND-WING. IN HIND-WING $SC + R_1$, WITH FEW EXCEPTIONS, PARTLY FUSED WITH RS BEYOND THE CELL AND M_1 STALKED WITH OR APPROXIMATED TO RS. OR, EACH WING DIVIDED INTO NOT MORE THAN FOUR PLUMES, AND HIND-WING WITH DOUBLE ROW OF SPINE-LIKE SCALES AT EDGE OF CELL ON VENTRAL SURFACE.

Table of families:

1	(2).—Wings almost always divided into plumes: with spine-like scales on ventral surface of hind-wing.	Pterophoridæ (p. 454)
2	(1).—Not as above.	
3	(4).—Cu_2 absent from hind-wing: $Sc + R_1$ not fused with Rs: tympanal organs absent.	Thyrididæ (p. 452)
4	(3).—Cu_2 present in hind-wing $Sc + R_1$ partly fused with Rs: tympanal organs present.	**Pyralina** (p. 453)
5	(10).—Hind-wing with cubital pecten on upper side.	
6	(9).—Fore-wing with R_5 present.	
7	(8).—Maxillary palpi strongly triangularly dilated with scales.	Crambidæ (p. 453)
8	(7).—Maxillary palpi filiform.	Galleriidæ (p. 453)
9	(6).—Fore-wing with R_5 absent.	Phycitidæ (p. 453)
10	(5).—Hind-wing without cubital pecten.	
11	(12).—Fore-wing with R_5 stalked with R_3 and R_4.	Pyralidæ (p. 453)
12	(11).—Fore-wing with R_5 free.	Pyraustidæ (p. 453)

The Pyraloidea form an enormous assemblage of small to medium-sized moths of fragile slender build and with relatively long legs. The approximation, or partial fusion, of $Sc + R_1$ with Rs in the hind-wings (Fig. 435) readily separates them from any other major division of Lepidoptera. Their larvæ have very varied habits, and many live in concealment. They are markedly active, and often exhibit a forward and backward wriggling motion when disturbed. They are usually slender and nearly bare, with little or no colour pattern. The abdominal feet are short, and provided with either a pair of transverse bands, or a more or less complete circle of biordinal crochets. The pupæ are not protruded from the cocoon in emergence, and abdominal segments 5 to 7 are free. Maxillary palpi are always present, and the surface of the body is seldom roughened with spines or setæ except in the Pterophoridæ.

FAM. THYRIDIDÆ.—A small tropicopolitan family of particular interest on account of the relationships which it exhibits with other of the larger groups of the Lepidoptera. Both Hampson and Meyrick claim that they are the ancestral group from which the butterflies have been derived. They are mostly small moths resembling Pyralids or Geometrids in general appearance, and can usually be recognized by the presence of white or yellowish translucent areas on the wings. They are widely distributed in the tropics but only 3 genera, embracing four species, are listed by Staudinger and Rebel as entering the Palæarctic region, *Thyris* alone being European. *Rhodoneura* Guen. includes over 100 species distributed from the W. Indies and S. America, through S. Africa and the whole Oriental region, to Australia. The larvæ, so far as known, exhibit Pyralid characters. For a revision of the family vide Hampson (*Proc. Zool. Soc.* 1897).

Related to the Thyrididæ are the small Indo-Australian families **TINEODIDÆ** and **OXYCHIROTIDÆ.** In the latter family *Cenoloba* has each wing divided into two plumes.

Pyralina

FAM. GALLERIIDÆ.—The Galleriidæ are a small but widely distributed subfamily whose larvæ feed on a variety of dried substances, including the combs of beehives and of wasps' nests, dried fruits, and in a few cases in roots, beneath bark, etc. Pupation takes place in a peculiarly tough cocoon. The best known species is the Bee moth, *Galleria mellonella* L., which has become artificially spread among hives in many parts of the world, including Australia. The biology and method of nutrition of this species have been studied by Metalnikov (*Arch. Zool. Exp.* 1908).

FAM. CRAMBIDÆ.—This family includes the Grass Moths, of which the genus *Crambus* comprises about 400 species (29 British). They are small insects with narrow elongated fore-wings and porrected labial palpi. They are extremely abundant in grass land and rest by day in an upright position with the wings folded on the stems. Their larvæ usually feed in silken galleries on grasses, reeds and allied plants, or on moss. Among other forms *Diatræa saccharalis* is the American sugar-cane borer and species of *Chilo* are similar pests in India.

FAM. PHYCITIDÆ.—The Phycitidæ are a very large group with elongate fore-wings which lack vein R_5: the hind-wings have, on the dorsal side, a well-defined pecten of hairs on the lower margin of the cell near the base. These insects are exceptional in that the frenulum is simple in both sexes. Secondary sexual characters are well seen in the swollen basal antennal joint of the males, and the same sex is often provided with a conspicuous row, or tuft, of hairs or scales on the fore-wings. The larvæ vary greatly in habits and usually live in silken tubes by day, coming out to feed at night. Nearly 50 species of the family are British, and over 800 are found in the palæarctic region. *Ephestia* Gn. includes the Mediterranean Flour Moth (*E. kuehniella* Z.), whose larvæ are great pests in flour mills; those of other species attack dried fruits, biscuits, and other commodities, *E. cautella* Walk. being the nearly cosmopolitan Fig Moth. The Indian-meal moth (*Plodia interpunctella* Hubn.) is even more widely distributed and attacks maize, figs and seeds of various kinds. *Lætilia coccidivora* is remarkable on account of its predaceous larva which lives upon various Coccidæ in N. America. A detailed study of the metamorphosis and larval and pupal structure of a Phycitid is given in Beeson's paper (*Ind. Forest Rec.* 8, 1910) on the Oriental Toon Moth (*Hypsipyla robusta* Moore), which is a shoot-borer. Larvæ of various other genera live in rolled or spun leaves, others affect flower-heads, and many live on the bark of trees. The Anerastinæ, which have a vestigial proboscis, are often regarded as a separate family.

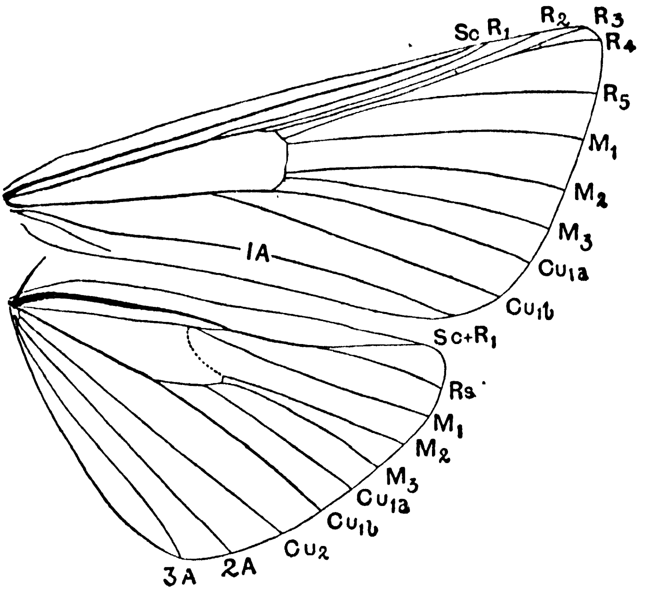

FIG. 436.—*Botys ruralis*, VENATION.

FAM. PYRALIDÆ.—This family is fairly numerous in the tropics, but scarce elsewhere, and absent from New Zealand. The larvæ feed, as a rule, upon dry or decaying vegetable substances. Those of the cosmopolitan *Pyralis farinalis* L. form silken galleries among corn and flour débris; species of *Aglossa* Latr. mainly live among hay and chaff refuse, while *Synaphe angustalis* Schiff. frequents damp moss. The subfamilies Chrysauginæ, Endotrichinæ and Epipaschiinæ are often regarded as separate families.

FAM. PYRAUSTIDÆ (Fig. 436).—These form an immense family, which includes most of the larger Pyralina. They are all characterized by R_5, in the fore-wing, arising separately from the cell, but are frequently divided into a number of families based upon relatively trivial characters. The Schenobiinæ have the proboscis vestigial and their larvæ live among aquatic plants. The anomalous genus *Acentropus* is the most truly aquatic of all Lepidoptera, and its structure and biology has been studied in detail by Nigmann (1908). The young larva tunnels in the petioles of *Potamogeton* and other water plants; it subsequently constructs a tube of portions of leaves spun together, but open at the two extremities. A cocoon is spun in a rather similar leaf-shelter, the pupa being almost completely submerged. Respiration in the larva appears to be cutaneous at first and it is only in the later stages that the tracheæ become filled with air. The females are dimorphic: the long-winged forms are aerial while those with reduced wings live entirely in the water, using their alary organs for swimming. The Nymphulinæ are of special interest for the reason that some species are also aquatic. In the genus *Nymphula* Sch. and *Hydrocampa* Latr., the larvæ are usually leaf-miners at first and live throughout life below the surface of the water. Their biology has been frequently studied, notably by Miall (*Aq. Ins.*), Muller (*Zool. Jahrb. Syst.* 1892) and Welch (*Ann. Ent. Soc. Am.* 1916). Two definite larval types occur; those without gills when mature (*H. nympheata*), and those in which such organs are present (*N. striatiotata*, etc.). The life-history of *N. maculalis* Clem. has been studied by Welch, who states that tracheal gills are wanting in the first instar but increase numerically after each moult. The pupa is enclosed in a silken cocoon on the submerged surface of a leaf, and the imago is not affected by contact with water during emergence. The method of respiration in this genus requires further study: during early life it is cutaneous and spiracles, if present, are closed. In *H. nympheata* and also in *Cataclysta lemnata* respiration subsequently takes place by open spiracles. In other species it is performed by means of tracheal gills: non-functional spiracles co-exist with the latter in *N. stratiotata*, but apparently not in *N. maculalis*.

The Scopariinæ are a small group characterized by a raised tuft of scales in the cell of the fore-wing. The large genus *Scoparia* mostly inhabits temperate regions and is extensively developed in New Zealand. The larvæ feed on moss and lichen, among which they form silken galleries. The Pyraustinæ are the largest group with 68 British species, and differ from the Scopariinæ in the absence of raised scales from the fore-wings. They are common in nearly all parts of the world and are exceedingly abundant in the tropics. Their larvæ usually feed in a slight web amongst spun-up leaves, or in stems, fruits or roots. The most notorious species is the European Corn Borer (*Pyrausta nubilialis*), which is an introduced pest of corn (maize) in Ontario and the eastern U.S.: although abundant on the continent of Europe, it is a rare immigrant in Britain.

FAM. PTEROPHORIDÆ (Plume Moths).—These insects are readily distinguishable by their deeply fissured wings; the anterior pair is longitudinally cleft into two, or more rarely three or four divisions, and the hind pair into three. There are no maxillary palpi, and all the species are extremely lightly built with very elongate fore-wings, and unusually long and slender legs armed with prominent tibial spurs. The species are nowhere numerous and 32 inhabit the British Isles. *Agdistis* Hub., and two other genera, are exceptional in possessing undivided wings. The larvæ mostly feed exposed on flowers and leaves but sometimes internally in stems or seed vessels the Compositæ being more frequently selected than any other order of plants. They are long and cylindrical with numerous secondary setæ. The abdominal feet are long and stem-like with uniordinal crochets. The pupæ (vide Chapman, 1896) are attached by the cremaster and occur above ground, sometimes in a slight cocoon. The body is roughened with short spines or with small groups of longer barbed spines arising from small elevations. Unlike the Pyralidæ, there are no maxillary palpi, and the deep furrow between the 9th and 10th abdominal terga is likewise absent. Among British species one of the commonest is *Pterophorus pentadactylus* L. whose larva feeds upon *Convolvulus*: the larva of *Agdistis bennetii* Curt. selects *Statice limonium* and that of *Trichoptilus paludum* Zelb. feeds upon the leaf-tentacles of *Drosera* (Chapman, *Trans. Ent. Soc.* 1906).

Superfamily **Psychoidea**

MAXILLARY PALPI ABSENT OR VESTIGIAL. PROBOSCIS USUALLY ATROPHIED. TYMPANAL ORGANS WANTING. POSTERIOR TIBIAL SPURS VERY SHORT WITH MIDDLE SPURS OFTEN ABSENT. BOTH WINGS WITH Cu_2 PRESENT (RARELY WANTING IN FORE- OR HIND-WING ONLY) AND M ALMOST ALWAYS PRESENT WITHIN THE CELL. HIND-WING WITH $Sc + R_1$ REMOTE FROM RS BEYOND THE CELL.

Table of families:

1 (2).—Hind-wings with Sc + R_1 coincident with the cell to middle or near extremity: palpi absent. Megalopygidæ (p. 456)
2 (1).—Not as above.
3 (6).—Hind-wings with Sc + R_1 anastomosing with the cell: palpi present.
4 (5).—Frenulum absent. Chrysopolomidæ (p. 456)
5 (4).—Frenulum present. Cochlididæ (p. 456)
6 (3).—Hind-wings with Sc + R_1 free or connected with the cell by a bar.
7 (12).—Proboscis absent.
8 (9).—Fore-wings with Cu_2 absent; females winged. Teragridæ (p. 456)
9 (8).—Fore-wings with Cu_2 present: females apterous.
10 (11).—Females and larvæ case-dwellers. Psychidæ (p. 455)
11 (10).—Females and larvæ not case-dwellers. Heterogynidæ (p. 456)
12 (7).—Proboscis present.
13 (14).—Antennæ clubbed: hind-wings with Sc + R_1 diverging from the cell from the base. Castniidæ (p. 457)
14 (13).—Antennæ filiform, rarely terminally dilated: hind-wings with Sc + R_1 approximated to the cell and connected by a bar. Zygænidæ (p. 456)

FAM. PSYCHIDÆ (Bag-worm Moths).—A somewhat small family with an extremely wide distribution: about 150 species occur in the palæarctic region but very few are British. The family has evolved along totally different lines in the two sexes, the males being highly specialized and swift fliers, while the females include the most degenerate of all Lepidoptera (Fig. 437). In the former sex the wings are thinly clothed with hairs and imperfect scales, and are almost devoid of markings. The labial palpi are very short, the antennæ are strongly bipectinated, and the frenulum exceptionally large. The females are always apterous, but exhibit various degrees of degeneration: in extreme forms the antennæ, mouth-parts, and legs are totally wanting. The larvæ inhabit cases which exhibit great variety of shape and of materials used in their construction: they carry their cases with them as they move about their food-plants. These habitations are formed of silk covered with fragments of leaves, twigs, grass and other objects. In *Apterona* they are wholly constructed of silk and

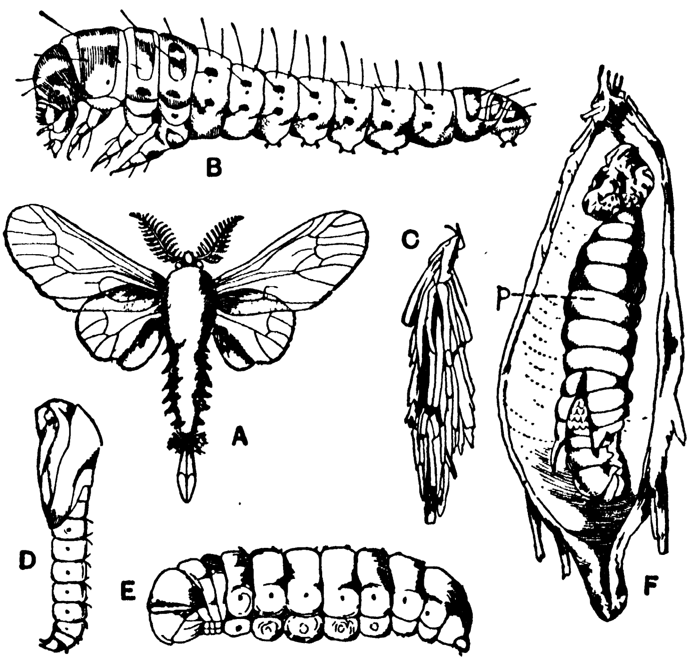

FIG. 437.—*THYRIDOPTERYX EPHEMERÆFORMIS.*

A, male imago; *B*, larva; *C*, larval "bag"; *D*, male pupa; *E*, female pupa; *F*, female imago within "bag"; *p*, pupa case. All enlarged. Adapted from Howard and Chittenden, *U.S. Bur. Entom. Circ.* 97.

are extremely close copies of Helix-like shells. Pupation takes place within the larval case, and the pupæ are provided with a row of sharp spinules on the abdominal segments. There is much diversity of structure in the female pupæ: thus according to Heylaerts wings are present in *Fumea*, while in *Thyridopteryx* Stph. and *Oiketicus* Guild. there are no traces either of these organs or of antennæ, maxillæ, or eyes and only slight vestiges of legs are present (Mosher). The imago of this sex is little more than an egg-sac and spends her whole life within the larval habitation. Copulation takes place by the male alighting on the case and inserting his protrusible abdomen between the wall of the former and the ventral surface of the female. *Fumea* is exceptional in that the female emerges from the case prior to copulation. Parthenogenesis is known to occur in *Apterona crenulella* var. *helix* but it is extremely doubtful if it is the rule in other species. Heylaerts (1881) has monographed the European species and gives much general information on the family: for the habits and structure of *Acanthopsyche opacella* H. Sch., vide Chapman (1900). The affinities of the Psychidæ appear to lie with the Heterogynidæ, and Heylaerts regards them as being intermediate between this family and the Lymantriidæ; other naturalists claim that they are also connected through the Heterogynidæ with the Zygænidæ. The larvæ of a few species are pests of fruit or other trees in N. America, S. Africa, etc.

The **HETEROGYNIDÆ** are an extremely small family represented by the southern European genus *Heterogynis* Rbr. The larvæ are not case-bearers, and the females resemble those of the Psychidæ in being vermiform and degenerate. They are stated to remain in the cocoons and lay their eggs there.

The **CHRYSOPOLOMIDÆ** are similarly a very small family comprising only two genera and about 24 species which inhabit parts of Africa.

FAM. TERAGRIDÆ (Arbelidæ).—A small tropical family of Ethiopian and Oriental range whose larvæ, so far as is known, are wood-borers. The moths are nocturnal and closely resemble the Cossidæ, but have a more reduced type of venation.

FAM. MEGALOPYGIDÆ (Lagoidæ).—An essentially American family with only few palæarctic species which occur in Africa. Their affinities apparently lie nearest to the Cochlididæ, particularly with regard to larval characters. According to Dyar their larvæ possess two series of abdominal feet. The normal ones occur on segments 3 to 6 and on 10, and are provided with crochets; the secondary feet lie on segments 2 to 7 and are of the nature of sucker discs. Mosher states that in *Lagoa* the pupa has the head and thoracic segments free, and abdominal segments 1 to 6 are free in the female, with segment 7 also in the male. The whole pupal covering is thin and membranous with the appendages entirely free from each other and from the body-wall. The cocoon is furnished with a circular operculum to allow of the emergence of the imago. An account of the metamorphoses and anatomy of *Lagoa crispata* is given by Packard (1894).

FAM. COCHLIDIDÆ (Limacodidæ, Heterogeneidæ or Eucleidæ).—A small family allied to the Zygænidæ and Megalopygidæ and including less than 40 palæarctic species: *Heterogenea* Knoch and *Cochlidion* Hb. are British. Their larvæ are commonly known as "slug caterpillars," which have thick, short fleshy bodies, a small retractile head and minute thoracic legs. Segmentation is indistinct and there are no abdominal feet, but according to Chapman (*Trans. Ent. Soc.*, 1894) secondary sucker discs are present on the first eight abdominal segments. A valuable series of papers on the structure of these anomalous larvæ has been contributed by Dyar (1895–9). Those of different genera have very little in common beyond the features enumerated: many are smooth and glabrous while others are provided with a conspicuous armature of spine-bearing scoli which, in the case of *Empretia stimulea*, are said to be poisonous. The pupæ strongly resemble those of the preceding family and are enclosed in a hardened oval or round cocoon. The latter is provided with an operculum which is constructed by the larva and allows of the free escape of the imago (Fig. 438).

FAM. ZYGÆNIDÆ.—The members of this family closely resemble the Syntomidæ but are readily separable therefrom by the presence of Cu_2 in the hind-wings (Fig. 439). Many are very brilliantly coloured and there is considerable diversity of structure. They are diurnal in habit, with a slow heavy flight, and are inclined to be very locally distributed. The larvæ (Fig. 440) possess the full number of limbs, and, so far as known, they are short and cylindrical with numerous verrucæ from which arise short hairs; they live exposed on herbaceous plants. The pupæ are enclosed in tough elongate membranous cocoons above ground; owing to their great capacity for movement, they are enabled to work their way out prior to the emergence of the imagines.

The sub-family Zygæninæ is characteristic of the palæarctic region where it is represented by 12 genera and over 100 species; 2 genera and 10 species inhabit the

British Isles. *Zygæna* F. includes the "Burnets" which have the antennæ distally enlarged and *Ino* Lch. includes the brilliant metallic green "Foresters." The Chalcosiinæ are from the largest group and are essentially tropical, only two species entering the palæarctic region. Many species are butterfly-like with slender bodies and broad large wings; in *Elcysma* Butl. and *Histia* Fab. the hind-wings are tailed. The Phaudinæ are a small and very aberrant sub-family in which the mouth-parts are wanting. In *Himanopterus* Westm. the hind-wings are filiform as in the Nemopteridæ (p. 402) and there is no frenulum: the genus is placed by some authorities in a family of its own—the Himanopteridæ (Thymaridæ).

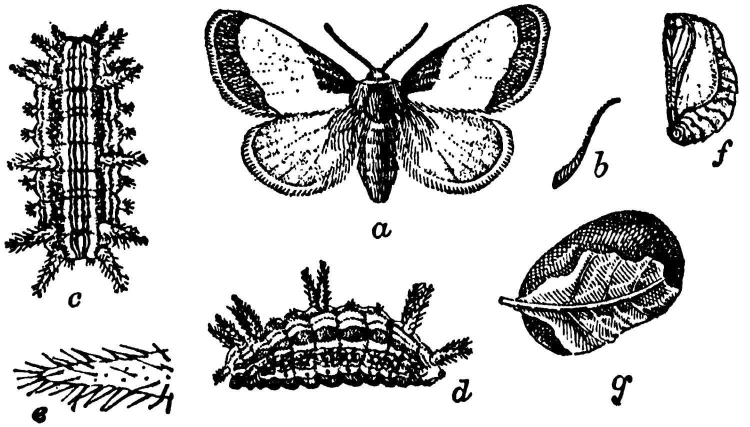

FIG. 438.—*Euclea indetermina*, N. America.

a, female imago; *b*, antenna of male; *c*, *d*, larva; *e*, scolus, much enlarged; *f*, pupa; *g*, cocoon. *After* Chittenden, *U.S. Dept. Agric. Ent. Bull.* 124.

FAM. CASTNIIDÆ.—Included in this family are a number of brightly coloured day-flying moths often bearing a resemblance either to Nymphaline butterflies or "Skippers"; they are confined to tropical America and the Indo-Malayan and Australian regions. Their metamorphoses have been very little studied. The eggs are upright and the larvæ feed within the stems of plants; for remarks on the pupa, vide Chapman (*Ent. Rec.* 1895). *Castnia licus* is destructive to sugar cane in tropical America and its metamorphoses are figured by Marlatt (*U.S. Dep. Agric. Ent. Bull.* 54). By some authorities the family is regarded as being closely related to the butterflies, but, with the removal of both *Megathymus* and *Euschemon* to the Hesperiidæ, the affinities appear to be less evident.

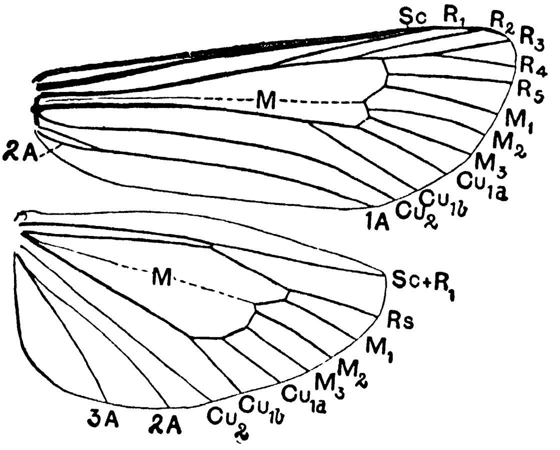

FIG. 439.—*Zygæna filipendulæ*, Venation.

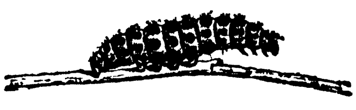

FIG. 440.—*Zygæna filipendulæ*. Larva, Nat. Size.

After Hampson (F.B.I.).

Mention needs to be made of the very minor families **DALCERIDÆ** and **RATARDIDÆ** found in the warm parts of America and the Orient respectively.

Superfamily **Bombycoidea**

MAXILLARY PALPI AND TYMPANAL ORGANS ABSENT. FRENULUM ALMOST ALWAYS ATROPHIED OR VESTIGIAL: PROBOSCIS RARELY DEVELOPED. ANTENNÆ GENERALLY PECTINATED, ESPECIALLY IN MALE. Cu_2 ABSENT FROM BOTH WINGS: HIND-WING WITH $Sc + R_1$ USUALLY DIVERGING FROM CELL AND RS, OR ONLY CONNECTED WITH CELL BY A CROSS-VEIN (R_1).

Table of families:

1	(2).—Hind-wing with costal area greatly widened basally and supported by usually two or more stout humeral veins from a subcostal cell between bases of Sc and R.	Lasiocampidæ (p. 458)
2	(1).—Not as above.	
3	(6).—Antennæ simple: fore-wing with M_2 basally approximated to M_3.	
4	(5).—Hind-wing with Sc + R_1, remote from Rs beyond the cell.	Pterothysanidæ (p. 461)
5	(4).—Hind-wing with Sc + R_1 closely approximated to Rs beyond the cell.	Callidulidæ (p. 461)
6	(3).—Antennæ generally pectinate in male: fore-wing with M_2 parallel to M_3 or approximated to M_1.	
7	(12).—Hind-wing with Sc + R_1 diverging from cell from base.	
8	(9).—Hind-wing with a rudiment of Cu_2, a vestigial frenulum: with two anal veins.	Lacosomidæ (p. 460)
9	(8).—Hind-wing without such vestiges: with one or two anal veins.	
10	(11).—With two anal veins: tibiæ with spurs.	Ceratocampidæ (p. 460)
11	(10).—Almost always with one anal vein: tibiæ without spurs.	Saturniidæ (p. 459)
12	(7).—Hind-wing with Sc + R_1 connected with cell by a cross-vein or basally approximated to Rs beyond the cell.	
13	(14).—Sc + R_1 connected with cell by a cross-vein: no proboscis.	Bombycidæ (p. 460)
14	(13).—Sc + R_1 basally approximated to Rs beyond the cell: proboscis present.	Brahmæidæ (p. 460)

The Bombycoidea or "frenulum-losers" are chiefly distinguished by the loss or the absence of characters. Their main feature is the atrophy of the frenulum and, correlated with it, the basal widening of the humeral area of the hind-wing. A frenulum occurs among the Callidulidæ and some Bombycidæ, but elsewhere only vestiges occasionally persist in the superfamily.

FAM. LASIOCAMPIDÆ (Eggars, Lappet-moths).—Usually moderate to large sized densely-scaled moths, with stout bodies, and the humeral lobe of the hind-wings prominent. The proboscis is atrophied, there are no ocelli, and the antennæ are bipectinated in both sexes. These insects are widely distributed but absent from New Zealand and are most abundant in the tropics. The eggs are smooth and oval, and the larvæ stout with a more or less dense clothing of secondary hairs which obscure the primitive setæ. They are often provided with lateral downwardly directed hairflanges, and hairy subdorsal tufts or dorsal humps on the anterior segments. The full number of abdominal limbs is present, and the crochets are biordinal arranged in a mesoseries. The pupæ resemble those of the Bombycidæ but differ in the presence of an epicranial suture and in the labial palpi being unconcealed. The body is provided with numerous setæ and there is no cremaster. A dense, rather firm, oval cocoon of hair and silk is commonly present and met with above ground.

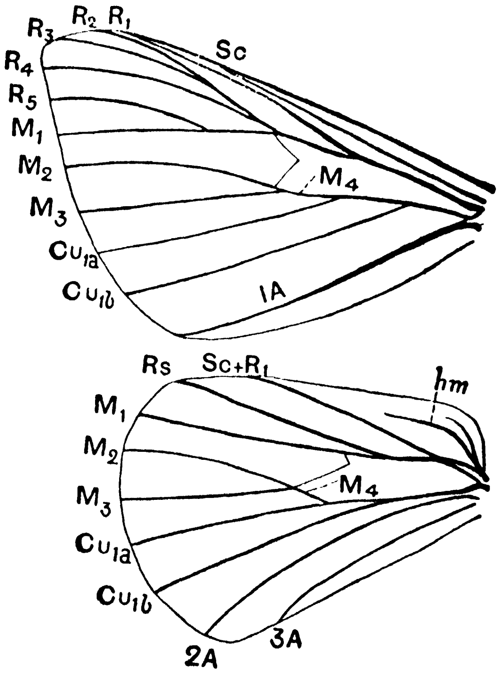

Fig. 441.—*Malacosoma neustria*, Venation.

Lasiocampa Schrk. is a small genus of large moths common in Europe and its species are usually swift fliers in sunshine: most members of the family, however, are nocturnal. *Malacosoma neustria* L. is the Lackey moth of Europe, whose larvæ live gregariously in webs during their earlier stages, and are very destructive to the foliage of fruit trees. The larvæ of *M. americana* have a similar habit and are commonly known as "tent-caterpillars," their webs measuring 2 feet or more in length.

FAM. SATURNIIDÆ.—In this family (which includes the Hemileucidæ) the antennæ are prominently bipectinate in both sexes, the rami being longest in the males; the labial palpi are minute and there is no frenulum. It includes a number of large, or very large, tropical insects with but few representatives in temperate regions: almost all are characterized by a transparent eye-spot near the centre of each wing. The only British species is the Emperor moth *Saturnia pavonia* L. (*carpini* Schiff.): *S. pyri* Schiff. is the largest European Lepidopterous insect. *Attacus* L. ranges from Mexico and S. America to Africa, and throughout the Oriental region to Japan. *A. atlas* L. (Fig. 442) and *A. edwardsi* White are among the largest moths in the world, the females having a wing-expanse of about 25 cm. Saturniad larvæ are very highly specialized (Fig. 443): they are stout and smooth and differ from most other families in possessing scoli or at least rudiments thereof. The position and number of the scoli vary very greatly in different genera, and for a detailed study of their arrangement reference should be made to Fracker's paper (1915); in *Saturnia* they are subequal in size on all the segments. The pupæ have the antennæ broadly pectinate in both sexes, with the axis of the flagellum very prominent. The maxillæ are always short, not more than ⅓rd the length of the wings, and the cremaster, if present, is very short. A dense firm cocoon is always formed and is very characteristic of the family: several species yield silk of commercial value. *Antheræa yamamai* Guer. is the Japanese oak silkworm which is reared on a large scale in that country, and was introduced into Europe in 1861. *A. pernyi* Guer., the Chinese oak silkworm, yields Shanting silk which is pale buff in colour and largely exported. *A. paphia* L. and *assama* Westw. are polyphagous forest-inhabiting insects. *A. paphia* is uni- or bi-voltine and very distributed through the oriental region: it yields the brownish Tasar silk. *A. assama* is a multivoltine semidomesticated species chiefly found in Assam: it yields Muga silk which is mainly used locally. *Philosamia ricini* Hutt. and *P. cynthia* Dru. are very closely related multivoltine species. The former is extensively domesticated and its larvæ are reared on *Ricinus communis*. It yields Eri silk which is white or brick-red but not reelable and is mainly used locally in Assam and Bengal. *P. cynthia* occurs wild in India and China but is also domesticated and has been introduced into various parts of the world including Europe and N. America. *Telea polyphemus* (N. America) also yields silk which can be commercially utilized. The biology of a number of species is described and their metamorphoses figured by Cotes (*Ind. Mus. Notes* 2, pt. 2) and by Andre ("Élevage des vers à soie sauvages"); notes on many silk-producing species are given by Wailly (*Entom.*

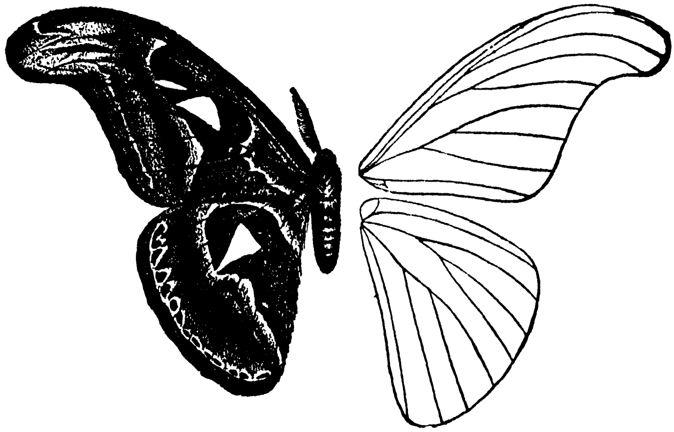
FIG. 442.—*Attacus atlas*, Male, India × ½.
After Hampson (F.B.I.).

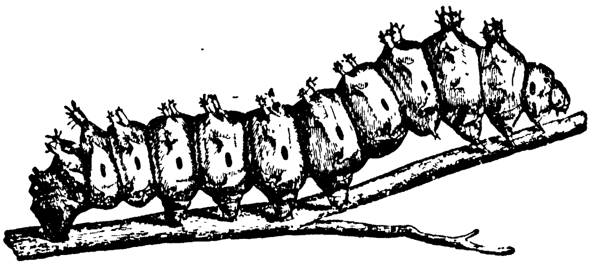
FIG. 443.—*Samia cecropia*, Larva.
After Riley.

1896–97) and for a full account of the Eri silkworm see Lefroy and Ghosh (1912). A good deal of information will also be found in Packard's monograph (1914) of the North America Saturniidæ.

FAM. BRAHMÆIDÆ.—A very small group of tropical moths related to the Saturniidæ, but readily distinguishable by the presence of a proboscis, and the large upturned labial palpi. They are large, sombre-coloured insects with very complex wing-patterns, and the antennæ are bipectinated in both sexes. *Brahmæa* Wlk. occurs in Africa and through southern palæarctic Asia to China: the life history is described by Packard (1914).

FAM. CERATOCAMPIDÆ (Citheroniidæ).—Large or medium-sized moths with stout hairy bodies, and powerful wings. The antennæ are bipectinate for about half their length only, and both proboscis and tibial spines are present. The family is a small one, unknown in Europe, but well represented in N. America. The larvæ are thinly hairy, and are armed with unbranched scoli on the 1st to 6th abdominal segments, and a large medio-dorsal scolus on the 8th segment. The pupæ are roughened with spines on the thorax and abdomen, the metathorax is provided with oblong lateral tubercles, and the cremaster is bifurcate. Transformation occurs in the ground, no cocoon being formed. For a monograph of the family vide Packard (1905, 1914): keys to the larva are given by Fracker (1915), and the pupæ have been studied by Mosher (1914).

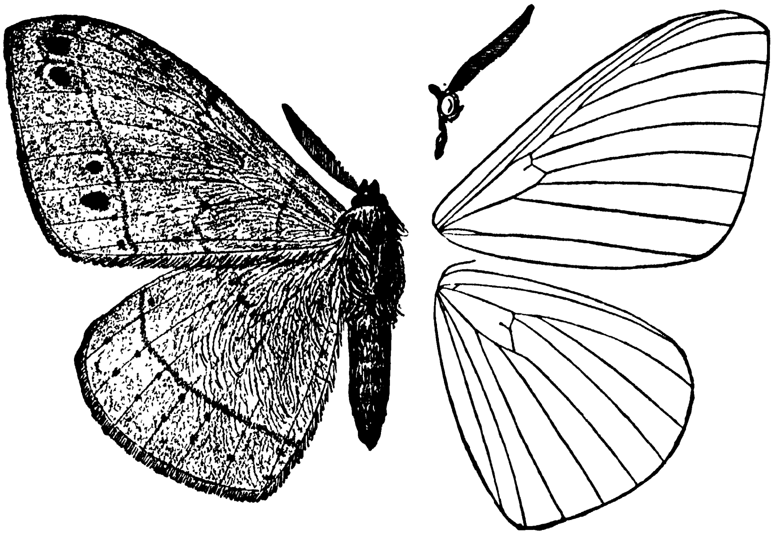

FIG. 444.—*EUPTEROTE FABIA*, MALE, INDIA. × $\frac{1}{1}$.
After Hampson (F.B.I.).

FAM. LACOSOMIDÆ (Perophoridæ).—These insects are moderate sized rather stout bodied moths found in N. and S. America. Their affinities are doubtful and they have been placed as exceptional members of the Drepanidæ or Psychidæ. They are remarkable on account of the larval habit of making suspended protective cases of the leaves of the food plants. In some instances the case is only constructed by the mature larva, the latter living previously under a web, and in at least one species the larva constructs a covering of its own excrement. There is a considerable literature on these larvæ and further information is given by Sharp (Ins. pt. 2). The life-history of *Lacosoma chiridota* Gr. is described by Dyar (*Journ. N. Y. Ent. Soc.* 1900).

FAM. BOMBYCIDÆ (including **Eupterotidæ**).—In this group a frenulum is usually present in *Eupterote* (Fig. 444) and its allies and absent in *Bombyx* and related genera. None are British and the family is mainly Ethiopian and Oriental. The antennæ are markedly pectinate in both sexes and the larvæ are of two types. In *Eupterote*, etc., they are tufted with long hair and secondary setæ are always numerous, but distinct verrucæ are wanting. In *Bombyx* and its allies the larvæ are glabrous and elongate, usually with a mediodorsal horn on the 8th abdominal segment: they form dense silken cocoons. The larva of *Bombyx mori* L. is the well-known silkworm, an inhabitant of China which has become introduced into many parts of the world for commercial purposes. It is now entirely domesticated and is not known in the wild state. A number of local races exist, and these have been regarded by Hutton, Cotes and others as distinct species. They differ chiefly in the number of annual broods which are largely dependent upon climate. The natural food in all cases is the leaves of mulberry, and the silk produced is white or yellow.

The **PTEROTHYSANIDÆ** include slender moths with large wing-expanse bearing a resemblance to Geometridæ. They are chiefly African, but the genus *Pterothysanus* inhabits the eastern Orient and is easily recognized by the long double hair-fringe which adorns the inner margin of the hind-wings. The related family **CALLIDULIDÆ** are day-flying moths, bearing a close resemblance to certain Thecline or other butterflies. The family is essentially Oriental and does not occur in Europe. The **ENDROMIDÆ** also require mention : the family includes only one species, *Endromis versicolor*, which is a rather large day-flying moth, widely distributed in N. and C. Europe but extremely local in Britain. It frequents the vicinity of woods, its larvæ feeding on birch and other trees. Seitz also includes with it the anomalous species *Mirina christophi* of Amurland.

Superfamily **Papilionoidea** (Fig. 426).

ANTENNÆ SLENDER, DILATED APICALLY FORMING A GRADUAL OR ABRUPT CLUB. LABIAL PALPI MODERATELY LONG, MORE OR LESS ROUGH-HAIRED, TERMINAL JOINT RATHER POINTED. MAXILLARY PALPI OBSOLETE. FORE-WINGS WITH CU_2 ABSENT, M_2 USUALLY ARISING FROM OR ABOVE MIDDLE OF TRANSVERSE VEIN. HIND-WINGS WITHOUT FRENULUM :[1] CU_2 ABSENT ; $SC + R_1$ ARISING OUT OF CELL NEAR BASE, THENCE STRONGLY CURVED AND DIVERGING.

This superfamily includes those insects commonly known as butterflies and are frequently regarded as constituting a group (Rhopalocera) of equal systematic value to the whole of the remainder of the Lepidoptera or moths (Heterocera). There is, however, no scientific justification for according to these insects any higher rank than that of a superfamily. They are characterized by the antennæ being clubbed or dilated, the absence of a frenulum and by the humeral lobe of the hind-wing being greatly developed. In other Lepidoptera the antennæ are not clubbed or dilated except in infrequent cases, and in such instances a frenulum is present. *Euschemon* is often regarded as a moth and either given separate family rank or placed in the Castniidæ. Recent research, however, indicates that it is probably the most archaic of all butterflies and a member of the Hesperiidæ. A frenulum is present in the male but absent in the female and, as Tillyard has pointed out (1918), if the nature of the wing-coupling apparatus be the criterion relied upon, the male of *Euschemon* is a frenate moth and the female a butterfly ! The Papilionoidea are a tolerably natural group, but there is no general consensus of opinion as to their phylogeny. Both Hampson and Meyrick regard them as being derived from the Pyraline family Thyrididæ while other authorities derive them from the Castniidæ.

Key to the families :

1	(10).—Fore-wings with two or more veins stalked or coincident : club of antennæ rounded.	
2	(5).—Anterior legs of male useless for walking.	
3	(4).—Anterior legs of female useless for walking.	Nymphalidæ (p. 462)
4	(3).—Anterior legs of female well developed.	Nemeobiidæ (p. 464)
5	(2).—Anterior legs of male well developed.	
6	(7).—Anterior tarsi of male more or less abbreviated or with one or both claws absent.	Lycænidæ (p. 464)
7	(6).—Anterior tarsi of male normal, claws developed.	
8	(9).—Hind-wings with a single anal vein.	Papilionidæ (p. 465)
9	(8).—Hind-wing with two anal veins.	Pieridæ (p. 465)
10	(1).—Fore-wing with all the veins present and separate : club of antennæ terminated by a recurved hook.	Hesperiidæ (p. 466)

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[1] Except in male of *Euschemon*.

FAM. NYMPHALIDÆ.—The dominant family of the butterflies and one of the largest of all Lepidoptera, including about 5,000 described species. The fore-legs in both sexes are reduced in size, usually folded on the thorax, and functionally impotent: the tibiæ are short and clothed with long hairs, hence the name of " brush-footed " butterflies.

The Danainæ (Euplœiinæ, Limnadidæ) have the antennal club often but little pronounced, and the whole antenna is devoid of scales: the fore-feet in the female terminate in a corrugate knob. The larvæ are smooth and cylindrical, with two to four pairs of fleshy processes, at least on the mesothorax, and often on one or more of the abdominal segments. They are all very strikingly marked with black and yellow, red, or green. The imagines have developed what must be, to our senses at any rate, an acrid disagreeable odour and taste, accompanied with a leathery consistency of body which evidently protects them from insectivorous enemies. In the majority of forms secondary sexual characters in the form of androconia, tufts of hairs, etc., having peculiar odours, are prominent (Bingham). The sub-family occurs in all warmer regions and well-known genera are *Danais*, *Euplœa* (Fig. 446), and *Amauris*.

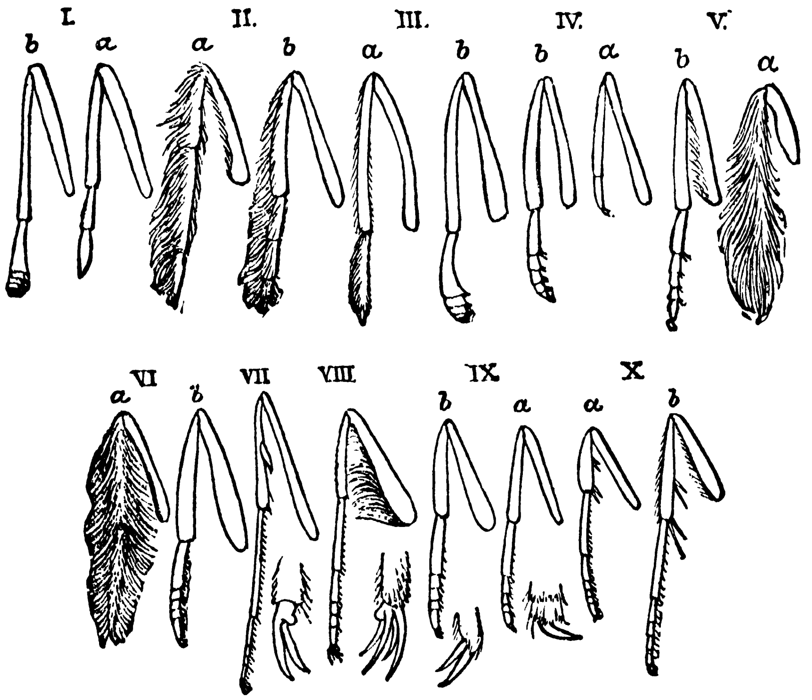

FIG. 445.—FORE-LEGS OF PAPILIONOIDEA.

a, male; *b*, female. I, Danainæ; II, Satyrinæ; III, Nymphalinæ; IV, Acræinæ; V, Libytheinæ; VI, Nemeobidæ; VII, Papilionidæ; VIII, Pieridæ; IX, Lycænidæ; X, Hesperiidæ. *After* Bingham (F.B.I.).

The Ithomiinæ differ from the Danainæ in that the female has a true though somewhat shortened fore-tarsus. The antennæ are devoid of scales and the wings are elongate, often in great part translucent, and thinly scaled. The sub-family is neotropical, and many species exhibit colour resemblances to the Heliconinæ or to the Pieridæ.

The Satyrinæ (Agapetidæ) are a world-wide group which includes the common " Meadow-browns," " Heaths," " Graylings " and " Marbled Whites." They are easily recognizable by certain of the veins at the base of the fore-wings being greatly swollen, and by the strongly adpressed palpi. They are small to medium-sized butterflies, frequently some shade of brown or tawny in colour, with a variable number of eye-like or annular spots. Their powers of flight are not greatly developed, and they are largely shade-loving insects, cryptically coloured on the underside. The larvæ feed mostly upon Gramineæ: they are fusiform and green, yellowish, or brown marked with longitudinal lines. In appearance they bear a resemblance to Noctuid larvæ. The head is often bilobed or horned, the prothorax constricted, and the body is clothed with small papillæ bearing short secondary setæ. The segments are divided into annulets, and the suranal plate is bifurcate, bearing a pair of short backwardly directed processes. The pupæ are similar in general form to those of the Nymphalinæ but are devoid of tubercles, and have few prominent ridges. They are generally suspended by the cremaster, and there is no median silken belt: a few are subterranean and, in some cases, they construct a slight cocoon or cell. *Erebia* is characteristic of the Alps of Europe, but also occurs on the mountains of Asia, S. Africa and N. America: two species inhabit N. Britain. In *Melanitis* F. the bases of the veins of the fore-wings are normal and not swollen. *M. ismene* Cram. extends across the southern half of Africa through the Oriental region to Australia: it has both wet and dry season forms and numerous local races. The Neotropical genera *Cithærias* and *Hætera* have delicate transparent wings, with the scales almost wanting.

The Morphinæ are exclusively tropical, and have the discal cell in the hind-wings open; there is also a cradle-like depression along their inner margins for the reception of the abdomen. The species of *Morpho* are large, and have an extensive wing-expanse in proportion to the size of the body. They are brilliant metallic blue insects peculiar to the forests of tropical America. The eastern representatives of the group do not equal their S. American allies either in size or brilliancy.

The Brassolinæ are likewise neotropical, and are very large insects with the discal cell of the hind-wings closed. They are deeply and richly coloured, and the under surface is marked with eye-spots and intricate lines. *Caligo* is one of the most familiar genera.

The Acræinæ are essentially African insects and the majority belong to the extensive genus *Acræa*: a few are Oriental and S. American. The wings are elongate and sparsely scaled, or more or less diaphanous. These insects appear to be largely immune from insectivorous enemies in all stages, and the imagines readily exude a nauseous fluid. The females in certain species develop an abdominal pouch very much as in *Parnassius* (vide p. 466).

The Heliconinæ form one of the most characteristic groups of neotropical butterflies and are peculiar to that region. The fore-wings are about twice as long as broad; the fore-tarsus in the male is elongate and single-jointed, and 4-jointed in the female. They are medium-sized insects, many of which are stated to be protected owing to possessing nauseous or evil-smelling properties. They are closely related to the Nymphalinæ in all their stages, but the imagines are readily distinguished by the closed discal cell.

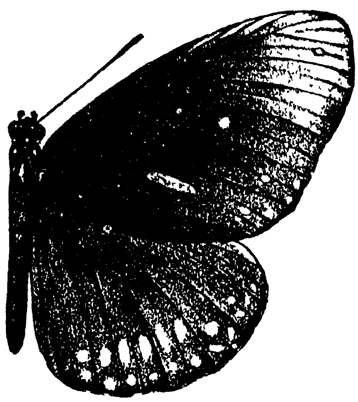

FIG. 446.—*EUPLŒA GODARTI*, MALE. INDIA × $\frac{1}{1}$.
After Bingham (F.B.I.).

The Nymphalinæ constitute the largest of the sub-families: the discal cell in both pairs of wings is very often open or closed only by an imperfect veinlet. The palpi are large and usually broad anteriorly. The fore-tarsi in the male are unjointed and in the female four or five joints are present. In Britain, as in most parts of the world, they constitute the dominant group of butterflies and include the "Fritillaries" (*Argynnis*, *Brenthis*, and *Melitæa*); the "Tortoiseshells" and "Peacock" (*Vanessa*); the "Purple Emperor" (*Apatura*) and other familiar insects. The larvæ are almost always cylindrical and armed with numerous scoli. In *Apatura* and *Charaxes* they are smooth with tentacle-like processes on the head, and a pair of posteriorly directed anal processes. Muller (1886) gives a very complete account of the metamorphoses of many Brazilian species, and discusses the significance of colour pattern and its relation to the scoli. The pupæ are very characteristic and are often armed with prominent tubercles on the surface of the body: there are usually seven rows on the abdomen, and there is a pointed projection on either side of the head in many species. The pupa is suspended head downwards by the cremaster, unsupported by a median girdle. Among the more notable species may be mentioned the central European *Araschnia levana* which produces two annual generations so dissimilar that they were formerly regarded as the two species, *A. levana* and *A. prorsa*. *Pyrameis cardui*, the "Painted Lady," is probably the widest distributed of all Lepidoptera. *Apatura* occurs over the northern hemisphere, and is represented in Britain by *A. iris*, which is local in oak woods of the southern counties. The Indo-Malayan *Kallima* includes the "leaf butterflies," remarkable on account of the extraordinarily perfect resemblance to leaves which is exhibited by the under surface of the closed wings. *Charaxes* includes large butterflies very widely distributed through the eastern hemisphere to Australia, and the hind-wings are produced at veins M_3 and Cu_{1b} into long slender tails.

FAM. NEMEOBIIDÆ (**Erycinidæ, Lemoniidæ**).—An extensive family comprising over 1,000 species which are characteristic of the neotropical region. A few species are found in the United States and approximately 100 occur in the eastern hemisphere. For the most part they are small butterflies, with short broad fore-wings, and the fore-legs in the male are imperfect and brush-like, with one-jointed tarsi devoid of claws: in the female the fore-legs are functionally perfect but distinctly smaller than the remaining pairs. The vast majority of the species belong to the sub-family Nemeobiinæ (Riodiniinæ) which has a single European representative, *Nemeobius lucina.* The latter insect extends its range into Britain where it is local but not rare. The Libytheiinæ may be easily recognized by the very long and closely approximated porrect palpi. The widely distributed genus *Libythea* includes a single palæarctic species *L. celtis*, which occurs in central Europe. The affinities of this sub-family have given rise to much discussion, and certain authorities relegate it to the Nymphalidæ while others regard it as forming a separate family. The Nemeobiinæ on the other hand are more nearly related to the Lycænidæ. The larvæ of the Libytheiinæ bear considerable resemblance to those of Pieridæ: each segment is divided into annulets, and numerous secondary setæ are present. The pupæ are short and smooth and suspended perpendicularly. Larvæ of the Nemeobiinæ exhibit marked diversity of form: in some cases they are onisciform, attentuated at the extremities, and covered with a variable development of secondary setæ. Both larvæ and pupæ resemble those of the Lycænidæ rather than any other family.

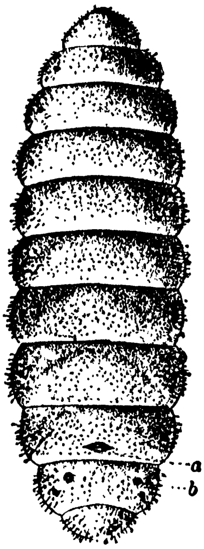

FIG. 447.—A LYCÆNID LARVA.

a, aperture of gland; *b*, one of the pairs of extensile organs. *After* Wheeler, "Ants."

FAM. LYCÆNIDÆ (Blues, Coppers, Hair-streaks).—A family of small to moderate-sized butterflies well represented in most regions. Over 280 species are palæarctic, and 18 have been recognized as British, though several are either no longer met with or are casual and extremely rare. The predominant colour of the upper surface of the wings is metallic blue or coppery, dark brown, or orange; on the under side coloration is more sombre, with dark-centred eye-spots or delicate streaking. The antennæ are ringed with white and a rim of white scales surrounds each eye; the hind-wings are frequently provided with delicate tail-like prolongations. The legs are all functional and used for walking but, in the males, the anterior tarsi are more or less abbreviated, or with one or both claws wanting. The sexes frequently exhibit great differences in coloration; thus in *Lycæna ægon*, for example, the male is purplish-blue and the female dark iridescent fuscous and, in *L. corydon*, the male is pale shining blue and the female iridescent brown. The great majority of the larvæ are onisciform, tapering towards the extremities, and with broad projecting sides concealing the limbs (Fig. 447). This type of body-form resembles that of *Zygæna* more than of any other Lepidoptera. Secondary setæ are usually numerous, but some larvæ are smooth or dorsally corrugated; many are clothed with a short pile, others are armed with bristle-bearing verrucæ and a few are hairy. The pupa is relatively short and stout, anteriorly rounded, and with little or no freedom of motion in the abdominal segments, which fit together to form a smooth surface. Generally it is attached at the anal extremity and secured by a central girth of silk: there are, however, a number of exceptions and in some cases the pupa is subterranean. For an account of the metamorphosis of several species of the family the student is referred to a series of papers by Chapman (*Trans. Ent. Soc.*, 1911–20). The larvæ in some cases are known to be carnivorous: that of *Gerydus chinensis* Feld. feeds upon aphides in China (Kershaw, *Trans. Ent. Soc.*, 1905). *Lycæna arion* (Europe) is phytophagous up to the last instar when it enters nests of *Myrmica* and becomes carnivorous preying upon the ant larvæ (Chapman, *Trans. Ent. Soc.*, 1915). The larva of the American *Feniseca tarquinius* is wholly carnivorous feeding upon woolly Aphids (*Eriosoma*, etc.), while that of *Spalgis epius* is recorded by Green as preying upon Coccids. Larvæ of other species are frequently sought after by ants, who use their antennæ to stroke them and induce them to yield drops of fluid secretion. The latter is apparently the product of a dorsal gland situated on the 7th abdominal segment (vide Newcomer, *Journ. N.Y. Ent. Soc.*, 20). The Indo-Australian *Liphyra brassolis* Westw. (Fig. 448) is the most remarkable member of the family, being totally unlike other forms in any of its stages (Chapman, *Entom.*, 1902, 1903). Its larva is flattened, and has a very hard smooth chitinized covering, devoid of evident segmentation : the jaws are sharply toothed and adapted for tearing and piercing rather than mastication. This curious larva is found associated with *Œcophylla smaragdina* and is believed to prey upon the brood of the latter, its hard covering serving as a protection against the ants. Pupation takes place in the larval skin : the pupa shrinks away from the cuticle and is loosely enclosed in the puparium thus formed. The newly emerged imago is covered with a number of loosely attached scales which may serve as protection against the ants, as they certainly cause the latter trouble when enveloped by them (Dodd, *Entom.*, 1902). *Euliphyra mirifica* Holl. similarly frequents nests of the same ant in W. Africa, and its greatly modified larva has been described by Eltringham (*Trans. Ent. Soc.*, 1913).

FAM. PIERIDÆ (Whites, etc.).—Included in this family are some of the very commonest of all butterflies ; they are mostly of medium size and usually either white, yellow or orange marked with black. The six legs are well developed and similar in both sexes, and the claws of the feet are bifid or toothed. Several taxonomists have united this family with the Papilionidæ, to form a single group, but the distinctness of the characters in the two cases does not appear to warrant this procedure. The larvæ are rather elongate with the segments divided into annulets, and the body bears numerous secondary setæ varying in size : the crochets are bi- or tri-ordinal arranged in a mesoseries. The larvæ are further characterized by the absence of osmeteria, fleshy filaments and cephalic or anal horns.

The pupæ are suspended in an upright position attached by the caudal extremity and a central band of silk : they may be readily distinguished by the single median cephalic projection or spine, and the hind-wings are not visible ventrally (Mosher). *Pieris* includes the common White or Cabbage butterflies whose larvæ, in several species, are extremely destructive to cruciferous vegetables in Europe and N. America. In this respect *Pieris rapæ* is probably the most injurious of all butterflies. Larvæ of other members of the family feed chiefly on plants belonging to the Leguminosæ and Capparidaceæ. *Euchlöe* and *Synchlöe* include the " Orange Tips," *Colias* the " Clouded yellows " and *Gonepteryx* the " Brimstones or Sulphurs ": all are characteristic of the northern hemisphere. Certain species of Pieridæ have the habit of migrating in large numbers, which has attracted the notice of travellers in many parts of the world. No satisfactory reason for these flights has been put forward : clouds of butterflies chiefly of *Appias* and *Catopsilia* may stream past the observer for hours at a time, all going in one direction (Bingham).

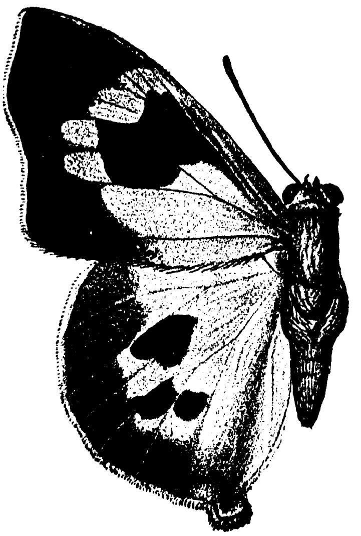

FIG. 448.—*LIPHRYA BRASSOLIS* × ½.
After Bingham (F.B.I.).

FAM. PAPILIONIDÆ (Swallow-tails).—An extensive family of pre-eminently tropical butterflies including some of the most magnificent of all insects. About 800 species are known ; less than 70 of these are palæarctic, and about 30 range into America north of Mexico. In the British Isles the sole representative is *Papilio machaon* which is local and now restricted to certain fenny districts in East Anglia. The wings of these insects are extraordinarily variable in shape and, in the majority of species, the hind pair is provided with conspicuous tail-like prolongations which are marginal extensions in the region of vein M_3. The prevailing ground colour is generally black, strikingly marked with shades of yellow, red, green or blue. The larvæ are smooth or provided with a series of fleshy dorsal tubercles or sometimes with a raised prominence on the 4th segment. Except in *Parnassius*, in which secondary setæ and verrucæ are evident, the body is practically devoid of setæ. An osmeterium is situated on the prothorax (vide p. 423) and when retracted its presence is revealed by a dorsal groove through which it is everted. The pupæ are variable in form : the head bears two lateral cephalic projections and the hind-wings are visible ventrally. Suspension takes place at the caudal extremity in an upright position, and the pupa is further secured by a median silken girdle. In *Thais* there is a cephalic as well as an anal attachment and *Parnassius* is exceptional in that the pupa is not suspended but occurs in a slight silken web among leaves. The imagines of many species of the family have the sexes extraordinarily different both in form and colour, and often in habits also. In numerous instances the females are polymorphic while, in other cases, this peculiarity extends to both sexes. As examples may be mentioned the Oriental *Papilio memnon* which has three distinct forms in each sex and two of these in the female are tailless. The North American *Iphiclides ajax* has three distinct seasonal forms, viz. those appearing in early spring, late spring and summer. The African *Papilio dardanus* (*merope*) is represented by different races or sub-species in various regions of that continent, and each of these possesses from one to five different forms of the female which, for the most part, are close mimics of certain Danaine butterflies. The greater number of the species of the family are included in the genus *Papilio*: those of the *Ornithoptera* group comprise the finest of all butterflies and they form the subject of a sumptuous monograph by Rippon (*Icones Ornithopterorum*). In the oriental genus *Leptocircus* the fore-wings have a transparent scaleless band, and the tails are exceedingly long. *Parnassius* occurs in the mountains of the holarctic region chiefly in Central Asia. Both pairs of wings are diaphanous, with few scales, and the tails are wanting. During copulation the females develop a corneous anal pouch exhibiting specific variations in form (Fig. 449). This genus also differs from other Papilionidæ in its venation and metamorphosis and, for this reason, is sometimes placed in a family of its own.

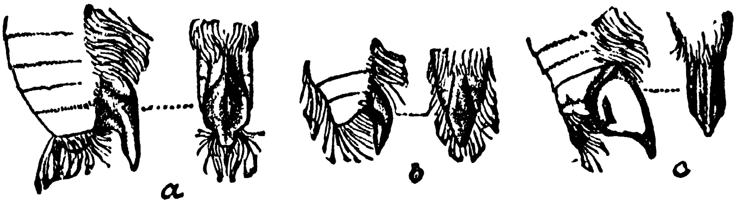

FIG. 449.—ANAL POUCHES (VENTRAL AND LATERAL ASPECTS) OF THREE SPECIES OF *PARNASSIUS*.

After Bingham (F.B.I.).

FAM. HESPERIIDÆ (Skippers).—These insects derive their popular name from their erratic darting flight which is different from the more sustained aerial evolutions of other butterflies. They form an extremely large family, generally distributed, but not ranging into New Zealand (vide Mabille and Boullett, *Ann. Sci. Nat.* 16; also Gen. Insectorum fasc. 17). The Hesperiidæ are the most distinct of all Papiionina and there is much to be said in favour of their separation to form a super-family of their own. Reuter regards them as constituting a sub-order—the Grypocera, but this view is based upon an exaggerated value ascribed to their distinguishing features. The antennæ are relatively widely separated at their bases, and their apices are generally prolonged beyond the club to form a small recurved point. The abdomen s stout, the wings are proportionately less ample than in most butterflies, and the venation of a markedly distinct type. As a general rule the larvæ are moderately stout and taper towards both extremities; secondary setæ are small, or absent dorsally, and the crochets are triordinal arranged in a circle. In the Hesperiinæ the head is large and attached to a strongly constricted "collar" while in the Megathymiinæ it is small and partially retractile (Fracker). They frequently live concealed, drawing together leaves by means of silk, or inhabit webs or galleries: those of the Megathymiinæ are borers. The pupa is devoid of angular points or projections and s usually enclosed in a slight cocoon among leaves: in other cases it is exposed and attached by the caudal extremity, and also by means of a median band of silk. The eggs are spherical or oval, flattened beneath, smooth or reticulated, and sometimes ribbed (Meyrick). The vast majority of the species belong to the Hesperiinæ and eight are indigenous to Britain. The Megathymiinæ include the Giant Skippers which have the apex of the antennæ devoid of a recurved point, and the wing veins are peculiarly specialized and greatly strengthened in the male. The group is mainly a tropical one and unrepresented in the palæarctic region. The Euschemoniinæ are often regarded as a family of moths, the males possessing a frenulum. *Euschemon* is the most archaic of all butterflies and according to Tillyard (1919) its larvæ and pupæ exhibit definite Hesperiid characters.

Superfamily **Geometroidea**

MAXILLARY PALPI VESTIGIAL OR ATROPHIED. TYMPANAL ORGANS IN BASE OF ABDOMEN. CU_2 ABSENT FROM BOTH WINGS: FORE-WING ALMOST ALWAYS WITH M_2 NOT NEARER M_3 THAN M_1 AT BASE AND WITH 1A + 2A FORMING A BASAL FORK.

Table of families:

1 (4).—Hind wings with $Sc + R_1$ approximated, or partly joined, to Rs beyond the cell.	
2 (3).—Fore-wing with M_2 basally approximated to M_3.	Drepanidæ (p. 467)
3 (2).—Fore-wing with M_2 not nearer M_3 than M_1 at base.	Cymatophoridæ (p. 467)
4 (1).—Hind-wing with $Sc + R_1$ remote from Rs beyond the cell.	
5 (8).—Fore-wing with $R_4 + R_5$ remote from $R_2 + R_3$ and usually stalked with M_1.	
6 (7).—Frenulum absent.	Uraniidæ (p. 468)
7 (6).—Frenulum present.	Epiplemidæ (p. 469)
8 (5).—Fore-wing with $R_4 + R_5$ connected with $R_2 + R_3$: hind-wing with $Sc + R_1$ furcate at extreme base.	Geometridæ (p. 467)

FAM. DREPANIDÆ (Drepanulidæ: Hook Tips).—A rather small family mainly developed in the Indo-Malayan portion of the oriental region. Its members exhibit considerable diversity of structure and, as a rule, have the apex of the fore-wing falcate. The eggs are rounded-oval with the surface finely punctured. The larvæ are somewhat slender without the claspers on segment 13, and the anal extremity is prolonged into a slender projection which is raised in repose; certain of the other segments are often humped. The pupa is enclosed in a cocoon, usually among leaves above ground. *Drepana* Schr. is the chief genus with 9 palæarctic species. *Cilex* Lch. has the fore-wings non-falcate, the frenulum is vestigial and there is no proboscis; *C. glaucata* Sc. is the only species and is holarctic in distribution.

FAM. CYMATOPHORIDÆ (Polyplocidæ).—A relatively small family resembling the Noctuidæ and mainly restricted to the northern hemisphere. Thirteen genera are palæarctic, four being represented by common species in the British Isles, the most familiar being the "Buff Arches" (*Habrosyne derasa*: Fig. 450) and the "Peach Blossom" (*Thyatira batis*). The larvæ are cylindrical and bear no secondary setæ: the abdominal feet carry biordinal crochets arranged in a curved mesoseries, and the claspers are reduced in size. Pupation occurs in a rather slight cocoon among leaves.

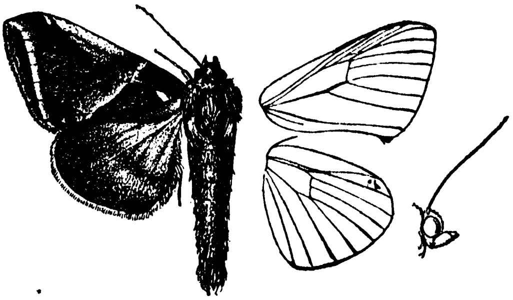

FIG. 450.—*HABROSYNE DERASA*, MALE, PALÆARCTIC REGION. × 1/1.
After Hampson (F.B.I.).

FAM. GEOMETRIDÆ (Carpets, Waves, Pugs, etc.).—A very large family consisting of several thousand species which are almost always of slender build with relatively large wings (Fig. 451). Their flight is never strong and, when at rest, the wings are often laid horizontally. Both frenulum and proboscis are generally present, but in a few cases either the one or the other may be wanting. In some genera the females have greatly degenerate wings or are completely apterous as in *Anisopteryx* Stph., *Cheimatobia* Stph., *Hybernia* Latr., *Phigalia* Dup. and certain species of *Biston* Lch. The larvæ are elongate and usually very slender: as a rule abdominal legs are only developed on the 6th and 10th segments and progression takes place by drawing the posterior somites close to those of the thorax, the body thus forming a loop. The whole body is then extended in the direction desired and the looping action repeated. In some instances abdominal legs appear on segments other than those normally carrying them. Thus in *Himera pennaria* a pair is present on the 5th segment but disappears with the fourth moult while in *Anisopteryx æscularia* they are developed on the same segment and persist throughout the larval period. In *Brephos notha* Sharp states that rudimentary abdominal feet are present on the 3rd to 5th segments in the newly hatched larva, but attain greater development when the latter is fully grown. It is evident that in this species the larva is much more a Noctuid than a Geometrid in its morphology. The vast majority of the larvæ of the family bear an exceedingly close resemblance to wigs, or the thicker veins of leaves, and can only be detected with difficulty when at rest. In the pupa there are no maxillary palpi, the first two pairs of legs are longer than in most other Lepidoptera, and there is often a deep dorsal furrow between the 9th and 10th abdominal segments. A slight cocoon is spun between leaves or the pupa is subterranean. The family is divided into six sub-families by Hampson while Meyrick (1895) regards each division as constituting a separate family under a different name. Over 3000 species occur in the palæarctic region and, of these, about 270 are British. In *Boarmia*, and its allies, a fovea is present on the underside of the fore-wing at the base of the anal region; it is generally confined to the male, is often hyaline and sometimes glandular. This structure is present in many species, and it is suggested by Meyrick that it may be a scent-producing organ. The posterior tibiæ, also in the male, are often enlarged and contain an expansible tuft of hairs. *Brephos*, *Anisopteryx* and a few other genera are regarded by Meyrick as being the most primitive of all Geometers and constitute his family Monocteniadæ. *Brephos* has also been referred to a family of its own, while other authorities have regarded it as a Noctuid. The larvæ of *Paleacrita* are known as Canker Worms which are pests of fruit and shade trees in N. America. Those of the Winter moth (*Cheimatobia brumata*) and of species of *Phigalia* and *Hybernia* are well known defoliators of similar trees in Europe.

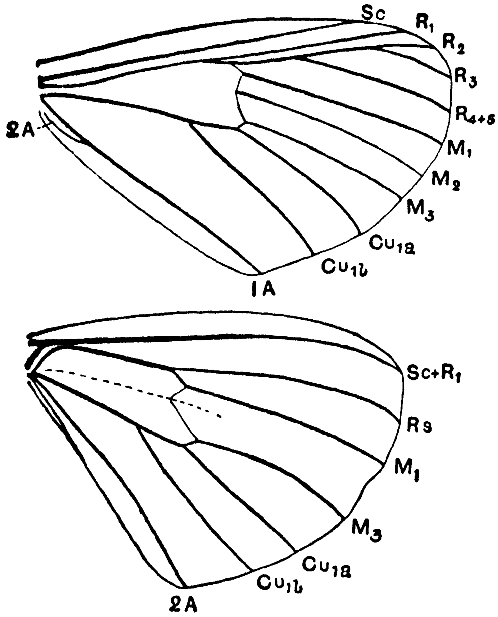

Fig. 451.—*Abraxas grossulariata*, Venation.

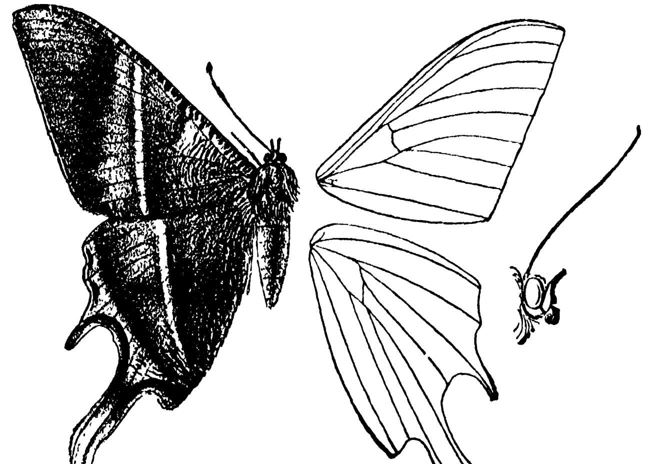

Fig. 452.—*Nyctalæmon patroclus*, Male, India. × ½. *After* Hampson (F.B.I.).

FAM. URANIIDÆ.—A very widely distributed but exclusively tropical family occurring in both the old and new worlds. They are often large slender-bodied moths, many of which are diurnal in habit. *Chrysiridia*, *Nyctalæmon* (Fig. 452) and *Urania* include exquisitely coloured insects resembling Papilionid butterflies: others bear a likeness to Geometrid moths. The larvæ exhibit great diversity of structure but have the full number of abdominal limbs (Hampson, 1895, vol. 3: Gosse, *Entom.* 14): in two genera they are known to feed on Euphorbiaceæ. Those of *Nyctalæmon* and *Epicopeia* are figured by Hampson: in *E. polydora* Westw. (Himalaya) the body is invested with a thick covering of long white cottony filaments. In *Chrysiridia ripheus* Dru. there is an armature of black spatulate processes (Eltringham, *Trans. Ent. Soc.*, 1923). The pupæ are enclosed in loosely woven, silken cocoons. The Asiatic genus *Epicopeia* Westw. has a vestigial frenulum and is often relegated to a separate family—the Epicopeidæ—which has been monographed by Janet and Wytsmann (*Gen. Ins.* 16).

FAM. EPIPLEMIDÆ.—A group of about 550 inconspicuous species, only doubtfully separate from the Uraniidæ. They occur on all continents but are greatest developed in Papua and adjacent islands. They commonly rest during the day with the fore-wings rolled up in a peculiar manner while the hind pair is applied to the sides of the body: in this attitude they resemble spiders.

Superfamily **Sphingoidea**

ANTENNÆ GRADUALLY THICKENED INTO A CLUB WITH THE APEX POINTED AND USUALLY HOOKED. PROBOSCIS AND FRENULUM ALMOST ALWAYS STRONGLY DEVELOPED. Cu_2 ABSENT FROM BOTH WINGS. FORE-WING WITH M_1 FROM STEM OF R_{3-5} OR BASALLY APPROXIMATED TO IT. HIND-WING WITH $Sc + R_1$ CONNECTED WITH CELL BY A CROSS-VEIN (R_1) AND APPROXIMATED TO RS BEYOND THE CELL. TYMPANAL ORGANS ABSENT.

A somewhat isolated group with a single family whose affinities lie toward the Notodontidæ.

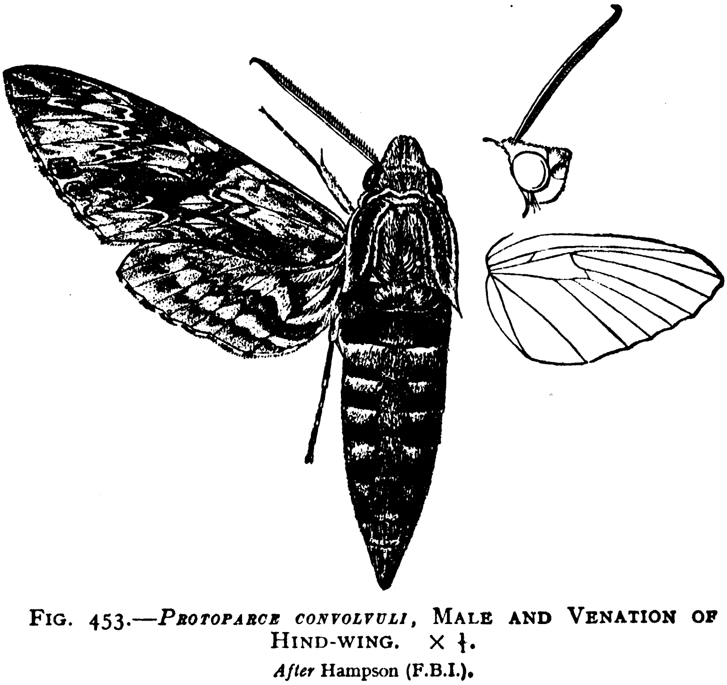

FIG. 453.—*PROTOPARCE CONVOLVULI*, MALE AND VENATION OF HIND-WING. × ½.

After Hampson (F.B.I.).

FAM. SPHINGIDÆ (Hawk Moths).—An important family of moderate-sized to very large moths, including at least 800 species, which are distributed over almost the whole world. It is essentially a tropical group which is represented in the British Isles by 8 genera and 17 species. *Deilephila lineata* F. is cosmopolitan and others such as *Acherontia atropos* L., *Daphnis nerii* L. and *Protoparce convolvuli* L. (Fig. 453) have a very wide geographical range. The imagines are easily recognizable by the elongate fore-wings and their very oblique outer margin. The antennæ are thickened towards or beyond the middle and are pointed at the apices which are nearly always hooked: in the male the antennæ are ciliated with partial whorls. The proboscis may be developed to a length which is not attained by any other Lepidoptera, but it is very variable. In *Cocytius* (tropical America) it measures 25 cm. long while the opposite extreme is found in *Polyptychus* in which it is reduced to a pair of tubercles. The frenulum and retinaculum are present in all generalized forms, but in some instances they are reduced or vestigial. In the Humming Bird moths (*Macroglossa*) and the Bee Hawk moths (*Hemaris*) the apex of the abdomen is provided with an expansile, truncated tuft of hairs. In the latter genus the disc of the wings is transparent, the fugitive scales present on newly-emerged specimens being very quickly lost. Sphingidæ have an exceptionally powerful flight and hover over flowers as they feed on the wing: most are crepuscular and nocturnal but a few (*Macroglossa, Hemaris, etc.*) are diurnal.

The larvæ are smooth, or with a granulated skin, but the latter feature is often only present in the first instar. The 8th abdominal segment almost always bears an obliquely projecting dorsal horn—relatively longer in the first than the later instars. The pupa occurs free in a cell in the ground, or in a very loose cocoon on the surface, between leaves, etc. The 5th and 6th abdominal segments are free and there is always a cremaster. Various methods of accommodating the proboscis are noticeable in the pupa and in some genera this organ projects from the body in a conspicuous manner so as to resemble the handle of a pitcher.

The Death's Head moths (*Acherontia*) are remarkable in several respects: the imagines have been noted to enter bee-hives to rob them of honey, and they possess the faculty of sound production. The note emitted is a shrill chirping sound and many hypotheses have been advanced to account for it. The literature thereon is fully discussed by Tutt (1899); the sound was originally attributed to friction but it seems probable that the real cause is the forcing of air through the proboscis, though the source of the air has not been ascertained (Rothschild and Jordan). The imago is occasionally audible before emergence from the pupa, but the larva emits a different type of sound. Most observers agree that when irritated it produces a series of rapidly repeated " cracking " notes resembling those emitted during the discharge of successive electric sparks, and the sounds are made by the mandibles when sharply brought together. The principal works on the family are those of Rothschild and Jordan (1903, 1907). For a general study of the larvæ, consult Forbes (*Ann. Ent. Soc. Am.*, 1911), while the larval colour changes and their significance are discussed by Piepers (*Tijd. Ent.* 40); for the life history of *P. convolvuli*, vide Poulton (1888).

Superfamily **Noctuoidea**

MAXILLARY PALPI MINUTE. TYMPANAL ORGANS PRESENT IN METATHORAX. CU_2 ABSENT FROM BOTH WINGS; FORE-WING USUALLY WITH M_2 BASALLY APPROXIMATED TO M_3 AND WITH 1A + 2A NOT FORMING A DEFINITE BASAL FORK.

Table of families:

1	(2).—Fore-wing with M_2 parallel to M_3 or approximated to M_1.	Notodontidæ (p. 470)
2	(1).—Fore-wing with M_2 basally approximated to M_3.	
3	(4).—$Sc + R_1$ fused with Rs.	Syntomidæ (p. 471)
4	(3).—$Sc + R_1$ not fused with Rs.	
5	(6).—Proboscis atrophied.	Lymantriidæ (p. 473)
6	(5).—Proboscis present.	
7	(8).—Hind-wings with $Sc + R_1$ anastomosing with the cell to near or beyond the middle.	Arctiidæ (p. 471)
8	(7).—Hind-wings with (*a*) $Sc + R_1$ anastomising with the cell near the base only or (*b*) connected with the cell by a bar.	
9	(12).—Hind-wings as in 8 (*a*).	
10	(11).—Antennæ with the shaft more or less dilated distally.	Agaristidæ (p. 471)
11	(10).—Antennæ with the shaft not dilated.	Noctuidæ (p. 471)
12	(9).—Hind-wings in 8 (*b*).	Hypsidæ (p. 473)

FAM. NOTODONTIDÆ (Prominents, etc.).—Insects with moderately stout bodies and rather elongate fore-wings: they are generally distributed but absent from New Zealand and poorly represented in Australia. The imagines are exclusively nocturnal, and are often attracted to a light, otherwise the various species are usually only obtained as larvæ. A large number of the larvæ of this family are well figured by Packard (1895); they mostly feed exposed on trees and shrubs, seldom affecting herbaceous plants. According to Fracker all exhibit secondary setæ on the abdominal limbs and, in some genera (*Phalera*, etc.), these setæ are present on the body also. The anal claspers are frequently modified into slender processes which are erected when in repose: the latter habit is also exhibited by *Notodonta* which has the claspers unmodified. The pupa only exhibits a small proximal portion of the labial palpi, maxillary palpi are absent, and the maxillæ do not reach the caudal margin of the wings: the abdomen is punctate and a cremaster usually present (Mosher). *Notodonta* O. is characteristic of the temperate regions of the northern hemisphere and in this genus, *Lophopteryx* Steph., and others there is a tuft of projecting scales on the middle of the hind margin of the fore-wings. *Stauropus* Germ. is Indo-Malayan with a single European species *S. fagi* L.: its larva is very remarkable on account of the great length of the 2nd and 3rd pairs of thoracic legs. The anal extremity is inflated and claspers are replaced by two slender processes. In repose both extremities are abruptly erected, and in the curious attitude thus presented the larva, when irritated, has been regarded by Müller as resembling a spider; when at rest it was compared by Birchall to a twig with unopened buds, and by other observers to a dead and crumpled leaf. The larva of *Dicranura vinula* L. is a very striking and familiar object: it is provided with a pair of roughened tubercles on the prothorax, and a prominent fleshy protuberance on the metathorax. The anal claspers are modified into a pair of long slender processes containing extensible filaments, and the histology and mechanism of these organs have been investigated by Poulton (1887). This larva, and also those of other members of the family, is provided with a ventral prothoracic gland (vide Latter, 1897) having the power of ejecting an irritating fluid. The latter in the case of *D. vinula*, has been found to consist of formic acid. The pupa in this species, and in those of *Cerura*, is enclosed in a hard woodlike cocoon on the bark of trees. The escape of the imago is facilitated by the cocoon being thinner anteriorly and the labrum of the imago bears two sharply pointed processes used for scraping the inner surface of the cocoon, in order to break a way through. At the same time, a secretion of potassium hydroxide is produced from the mouth in order to soften the cocoon. The eyes, and median portion of the head of the pupa, persist as a shield protecting those same parts in the imago until emergence is effected (Latter, 1892, 1895).

FAM. SYNTOMIDÆ (Amatidæ).—This family comprises about 2000 species and is most abundant in the tropics; no representatives are indigenous to the British Isles and *Syntomis phegea* L. is the commonest of the few European forms. They are small to medium-sized moths (Fig. 454), usually inactive and largely diurnal in habit. The proboscis is generally well developed, the labial palpi are small and porrect and the retinaculum bar-shaped. Although often included among the Zygænidæ, they appear to be nearest related to the Arctiidæ. Many are brilliantly coloured, and a number of species bear a striking resemblance to Aculeata, Tenthredinidæ and other insects (vide Kaye, *Trans. Ent. Soc.*, 1913). The resemblance is heightened by the frequently basally constricted abdomen and the general shape and coloration; in many cases the wings have transparent areas devoid of scales. In the neotropical genus *Trichura* Hubn. the males of certain species are provided with a long filamentous appendage arising from the terminal abdominal segment. This structure attains a length equal to that of the whole body of the insect, but its significance appears to be unexplained. The larvæ are short, and armed with verrucæ bearing numerous setæ and they closely resemble those of the Arctiidæ. Pupation takes place in a cocoon of silk and felted hairs: according to Mosher the pupa of *Ctenucha* is indistinguishable from that of an Arctiad.

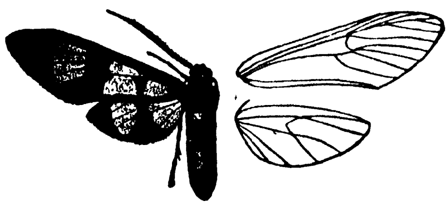

FIG. 454.—*Euchromia polymena*, Male, India. × $\frac{1}{1}$.
After Hampson (F.B.I.).

FAM. ARCTIIDÆ (Lithosiidæ: Tiger Moths, etc.).—An assemblage of usually stout-bodied moths, often with moderately broad wings, which are frequently conspicuously spotted, banded or otherwise marked with bright colours. Most species are nocturnal in habit and are attracted to a light. The family is tolerably well represented in nearly all zoo-geographical regions, but attains its greatest development in the tropics. Over 3500 species are known and, of these, 40 inhabit the British Isles. According to Meyrick (1895) *Callimorpha* is the most ancestral form, but it is placed by Hampson in the Hypsidæ. In its general affinities the family comes nearest to the Noctuidæ. It is noteworthy that species of several genera are known to be capable of sound production, but the mechanism thereof has not been adequately studied.

The Arctiinæ comprise the "Tiger" and "Ermine" moths with their allies. They are brightly coloured insects with extremely diverse patterns, and individual species exhibit an extraordinarily wide range of variation with respect to the latter. The extensive genus *Arctia* Schrk. includes the common "Tiger" moth (*A. caia* L.) which extends through the northern palæarctic region to Japan. *Deiopia pulchella* L., although casual in Britain, occurs through the greater part of the Old World including Australia. The larvæ are clothed with dense long hairs which they utilize along with silk to construct their cocoons; those of the palæarctic species hibernate and feed principally upon low herbaceous plants. The Lithosiinæ include those moths which are popularly termed "Footmen"; they are diurnal or crepuscular in habit and, in typical genera, the fore-wings are long and very narrow. The larvæ are sparsely hairy, and commonly feed upon lichens growing about tree trunks and in other situations. The Nycteolinæ are a very small group which is sometimes regarded as a separate family (Cymbidæ): they are frequently green insects found among the herbage of trees and shrubs. The larvæ are never prominently hairy and the cocoon is boat-shaped. In *Hylophila* Hb. (*Halias*) the larva is smooth and feeds in the open while in *Earias* Hb. it is hirsute and lives among rolled leaves, etc.; that of *E. insulana* Boisd. is the destructive Egyptian Cotton Bollworm, widely distributed in the tropics. The New World sub-families Dioptinæ and Pericopinæ are regarded as constituting separate families by American entomologists.

FAM. AGARISTIDÆ (Phalænoididæ).—A small family absent from Europe and including over 60 genera embracing about 300 species. They are largely tropical, only two palæarctic species being listed by Staudinger and Rebel; others occur in N. America and Australia. In general facies and vivid coloration they resemble the Arctiinæ and many are diurnal in habit (Fig. 455). They are very similar to the Noctuidæ in structure, and also in larval features, but their type of coloration and antennal characters serve to distinguish them. According to Hampson (*Proc. Zoo. Soc.*, 1892) in *Ægocera tripartita* Kirby a portion of the membrane of the anterior wing is dilated and ribbed; a clicking sound is produced during flight probably by friction on the greatly enlarged mid-tarsal spines.

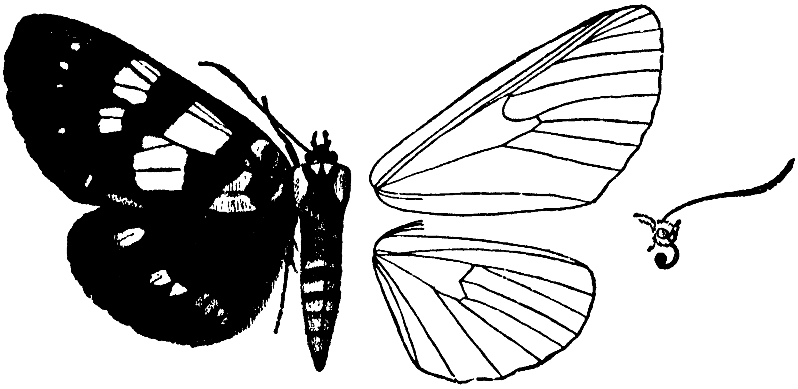

FIG. 455.—*EUSEMIA ADULATRIX*, FEMALE, INDIA. × ½.
After Hampson (F.B.I.).

FAM. NOCTUIDÆ.—This family includes a larger number of described species than any other group of Lepidoptera; about 1800 are palæarctic and approximately 3500 are known from N. America. They are eminently nocturnal insects attracted to a light and to the collector's sugar mixture, while *Plusia* and its allies frequent flowers at dusk. The family exhibits a monotonous similarity of structure particularly with regard to the venation and labial palpi; except in the Hyblæinæ maxillary palpi are vestigial. A frenulum is always present and the proboscis very rarely atrophied. The colour of the fore-wings is nearly always cryptic and sombre, thus assimilating the insect to its surroundings (Figs. 456, 457). Being protected in this manner it passes the day resting with folded wings on tree-trunks, etc., to a large extent concealed from its enemies. In the larvæ of the majority of species primary setæ only are present, and the crochets are generally in a uniordinal mesoseries. There are usually four pairs of abdominal feet, but among the Catocalinæ, Plusiinæ, and Hypeninæ the 1st pair, or the 1st and 2nd pairs, are more or less aborted and the larvæ are semi-loopers. Most of the larvæ feed upon foliage; they are often polyphagous and many are nocturnal while a few are stem-borers and live concealed. Among the more exceptional instances are the larvæ of *Eublemma* which are predaceous upon Coccidæ, those of *E. amabilis* being one of the most important enemies of *Tachardia lacca.* Species of *Bryophila* feed upon lichens; *Nonagria* in stems of marsh plants; *Parascotia* (*Boletobia*) *fuliginaria* L. utilizes fungi growing on rotting wood; and larvæ of *Dianthœcia* mostly select the seed capsules of Caryophyllaceæ. According to Mosher the pupæ, with few exceptions, are characterized by the presence of labial palpi and of maxillæ which extend to the caudal margin of the wings. Numerous genera have the prothoracic epimera exposed, and those lacking labial palpi possess setæ arranged around the scars of the larval verrucæ as in Arctiidæ. They differ from the latter, however, in that the cremaster bears hooked setæ. Pupation takes place as a rule in an earthern cell below ground, and the pupal cuticle is retained within the latter by the cremaster : in *Plusia* and its allies a cocoon is usually present and is spun between leaves, etc. The eggs of Noctuidæ are spherical and generally ribbed and reticulated.

Certain Noctuid larvæ (*Agrotis, Noctua*, etc.) are known as " Cut-worms " ; they are more or less abundant every year and in N. America rank among the worst of insect pests (vide Gibson, *Dept. Agric. Canada Ent. Bull.* 10). The larva of *Leucania unipuncta* Hw. is the notorious and almost cosmopolitan " Army Worm " so called from its habit of appearing in enormous numbers ; as food becomes exhausted these larvæ assume a gregarious marching habit seeking fresh fields. It is particularly injurious to cereals in the United States and Canada and for a full account of its habits vide Gibson (*Loc. cit. Bull.* 9). The larvæ of the Antler moth *Charæas graminis* comes under the same category, and is periodically exceedingly destructive to upland pastures in N.W. Europe ; the last severe outbreak in Britain took place in 1917 (vide *Journ. Bd. Agric.* 24). Among other destructive species is *Aletia argillacea* whose larva is the well-known Cotton Worm of N. America ; that of *Heliothis armigera* is the Boll Worm which is injurious to cotton bolls and the fruit of other economic plants on that same continent. *Hadena oleracea* has, in recent years, become a serious pest in tomato houses in England (vide Lloyd, *Ann. App. Biol.* 1920).

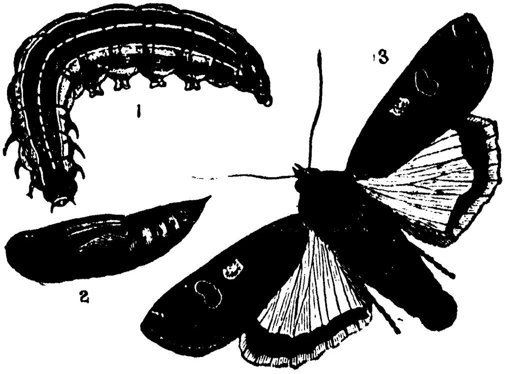

FIG. 456.—*AGROTIS PRONUBA*, EUROPE.

1, larva ; 2, pupa ; 3, imago × $\frac{1}{1}$. *After* Curtis, " Farm Insects."

FAM. LYMANTRIIDÆ (Liparidæ, Ocneriidæ: Tussock Moths).—The Lymantriidæ are mostly moderate-sized insects, rarely brilliantly coloured, and the antennæ of the males are very prominently bipectinate to the apex. The family is hardly distinguishable from the Noctuidæ on any venational feature : as a rule the bipectinate male antennæ, and the absence of ocelli, afford more easily recognizable characters. The caudal extremity of the female is often provided with a large tuft of anal hairs which are deposited as a covering for the egg masses. The larvæ are hairy, generally densely so, often with thick compact dorsal tufts on certain segments (Fig. 458). Osmeteria are frequently present on the 6th and 7th abdominal segments. Larvæ of the common European " Gold Tail " (*Porthesia similis* Fuess.) are provided with urticating hairs composed of barbed spicules. It appears uncertain whether their irritating properties are mechanical only, or are partly due to a poisonous secretion bathing these spicules. Eltringham (*Trans. Ent. Soc.*, 1913) has shown that the female collects the spicules, which are present on the cocoon, by brushing the latter with the anal tuft, and subsequently distributes them over the egg-mass. The pupæ are enclosed in cocoons above ground, and are characterized by the presence of very evident setæ arranged around the scars of the larval verrucæ. The best known member of this family is *Lymantria dispar* L., the common " Gipsy " moth of Europe, which was introduced into N. America about 1868 along with the Brown Tail (*Euproctis chrysorrhœa* L.). These species have now become serious pests of shade and foliage trees on that continent. ***Lymantria monacha*** is the " Nun " moth whose larvæ are often a serious pest in the forests of Germany. In *Orgyia* wings are vestigial or absent in the female (Fig. 458).

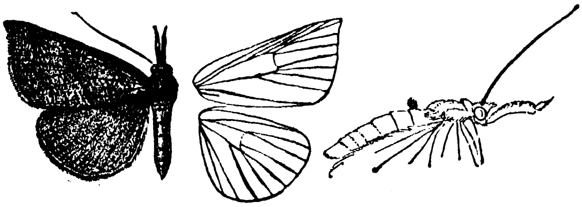

FIG. 457.—*HYPENA PROBOSCIDALIS*, MALE, PALÆARCTIC REGION. × $\frac{1}{1}$.

After Hampson (F.B.I.).

The **HYPSIDÆ** differ from the preceding family in the presence of a well developed proboscis. The larvæ are thickly covered with long hairs and construct a slight pupal cocoon. *Hypsa* Hubn. occurs in Africa, throughout the Orient and in tropical Australia. The **Thametopœidæ** are a very small Palæarctic family of few species, apparently allied to the Notodontidæ. The larvæ are tufted with long hair and secondary setæ are always numerous, but distinct verrucæ are wanting. Larvæ of *Thaumetopœa* Hb. (*Cnethocampa*) are known as processionary caterpillars which exhibit gregarious habits. *T. processionea* L. is the well-known European processionary moth. Its larvæ march in columns, each being headed by a leader, the column gradually becoming broader behind. It is believed that the individuals guide themselves and maintain their positions by means of threads spun by the leaders of each of the files. Brindley has observed these columns in the case of *T. pinivora* Tr. and conducted a series of experiments (vide *Proc. Camb. Phil. Soc.* 1910). He concludes, however, that the threads secreted by individuals on the march are of very slight importance either in forming the procession or maintaining its integrity. The larvæ endeavour to maintain head and tail contact with the members of their file and this appears to be of primary significance in forming the procession.

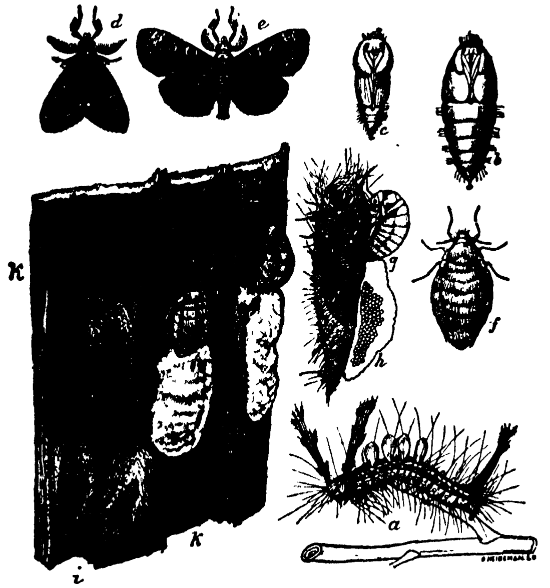

FIG. 458.—*Orgyia* (*Notolophus*) *leucostigma*.

a, larva; *b*, female pupa; *c*, male pupa; *d*, *e*, male imagines; *f*, female imago; *g*, same ovipositing; *h*, egg mass; *i*, male cocoons; *k*, female imagines ovipositing. Reduced from Howard, *Yearbook U.S. Dept. Agr.* 1895.

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Order 19. COLEOPTERA (Beetles)

MINUTE TO LARGE INSECTS WHOSE FORE-WINGS ARE MODIFIED INTO HORNY OR LEATHERY ELYTRA WHICH ALMOST ALWAYS MEET TO FORM A STRAIGHT MID-DORSAL SUTURE : HIND-WINGS MEMBRANOUS, FOLDED BENEATH THE ELYTRA, OR OFTEN REDUCED OR WANTING. MOUTH-PARTS ADAPTED FOR BITING : LIGULA VARIABLY LOBED. PROTHORAX LARGE AND MOBILE, MESOTHORAX MUCH REDUCED. METAMORPHOSIS COMPLETE : LARVÆ CAMPODEIFORM OR ERUCIFORM, SELDOM APODOUS : PUPÆ EXARATE.

The Coleoptera number approximately 250,000 described species and are consequently the largest order in the animal kingdom : about 3,600 species inhabit the British Isles. Although they are the predominant insects of the present epoch beetles do not meet the eye so frequently as members of other orders on account of their more concealed habits. Their adaptability, and the structural modifications which they exhibit have evidently contributed much to their dominance, for the imagines of no other order of insects have invaded the land, air and water to the same proportional degree. The habits of beetles, therefore, are extremely varied : they are more especially insects of the ground and either inhabit the soil itself, or the various decaying animal and vegetable substances present in relation to that medium. Dung, carrion, refuse of all kinds, humus, rotting wood and fungi all support large associations of Coleoptera. The members of five families are true aquatic insects while many other families have aquatic or subaquatic representatives. The Phytophaga and most Rhynchophora are usually met with in association with herbaceous plants, bushes and trees. Representatives of the most diverse families, whether they be aquatic or terrestrial, possess ample wings and readily take to flight. Several species are marine in that they are daily submerged by the tides. A considerable number of beetles occur in close relation with man since they are found in wool, furs, hides, furniture, museum specimens, and in dry stored foods and drugs. The great solidarity of the integument exhibited in the majority of species has been an important factor in protecting them against enemies of various kinds. The various sclerites are fitted together with a precision that marks them out as truly marvellous pieces of natural mechanism.

Included in the order are some of the largest and also some of the most minute of living insects. Among the Lamellicornia *Goliathus regius, Dynastes hercules* and *Megasoma elephas* attain a body-size not found outside the Coleoptera : *D. hercules* (including the cephalic horn) measures up to about 155 mm. long and the Longicorn *Macrodontia cervicornis* (including the mandibles) attains approximately the same dimension. On the other hand, among the Corylophidæ and Trichopterygidæ are insects so minute that they may reach a length of less than ·5 mm.

The literature on Coleoptera has assumed enormous proportions. For a general introduction to the study of the order the student should consult the work of Fowler (1912). For the British species the monograph by the latter author (1887–1913) is indispensable : the works of Reitter (1908–

16; 1909) and Kuhnt (1912) will also prove valuable for purposes of identification. The leading treatise on the European forms is that of Ganglbauer (1892–1904), but unfortunately it was never completed. The European Coleoptera are catalogued by Heyden, Reitter and Weise (1906) and the species of the world by Junk and Schenkling whose work (1910 etc.) is still in course of publication: Leng (1920) has catalogued the N. American species and his volume contains a very full bibliography of the systematic literature on the order. The British species are listed by Beare (1930) and the more recently added species are discussed by Donisthorpe (1931).

External Anatomy

The Head (Fig. 459).—The head is heavily chitinized and, as a rule the *epicranial suture* is incomplete or vestigial. A complete Y-shaped suture occurs, however, in the Hydrophilidæ but generally the epicranial suture is represented by the line demarcating the fronto-clypeus from the vertex (vide Stickney, 1923). In most of the Rhynchophora, and in a few isolated genera among other groups, the frons and vertex are prolonged anteriorly to form a *rostrum* (Fig. 462). The latter bears the mouth-parts at its apex and the antennæ are also carried forwards: as a rule the rostrum has a groove or *scrobe* on either side for the reception of the scape of the antenna. The *eyes* are very variable and may be totally wanting. Eyeless Coleoptera are met with among cavernicolous species and in certain subterranean forms, including those living beneath boulders. Eyes are similarly wanting in *Platypsyllus* and *Leptinus*. In the males of many of the Lampyrinæ the eyes are very large and contiguous, or nearly so, above and beneath: in the females they are often very small. Occasionally the eyes are partially or almost completely divided by a corneous ridge as in *Throscus* and *Dorcus*: or they may be completely separated into an upper and a lower eye on each side as in *Gyrinus* and *Amphiops*. *Ocelli* are rarely present but a pair of these organs are found in certain Staphylinidæ (Homaliinæ) and in *Pteroloma* among the Silphidæ. The *clypeus* is divisible into *ante-clypeus* and *post-clypeus*. The latter sclerite is fused with the frons and the dividing suture is wanting: the ante-clypeus is often infolded and not visible from above (Stickney). Among Rhynchophora the reduced fronto-clypeal region is often termed the *epistoma*. The *labrum* is very variably developed but is present in nearly all the families: it may, however, be concealed beneath the clypeus, or be absent, as in the majority of the Rhynchophora. The floor of the head, in the median line, is formed by the *gula* and the latter sclerite is marked off from the genæ, on either side, by the *gular sutures*. Among the Rhynchophora, and a few other beetles (*Necrophorus*, etc., Fig. 461), the gula is wanting and the genæ meet in the mid-ventral line, and there is consequently only a single gular suture present.

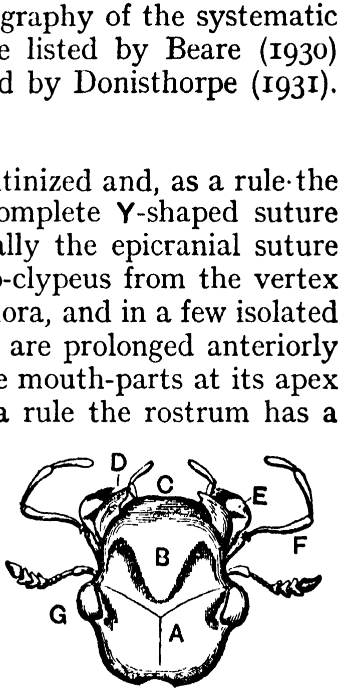

FIG. 459. — *HYDROPHILUS PICEUS*, DORSAL VIEW OF HEAD.

A, vertex; *B*, fronto-clypeus; *C*, labrum; *D*, mandible; *E*, maxilla and *F*, its palp; *G*, antenna. Adapted from Newport.

The *antennæ* exhibit a very wide range of variation and the usual number of joints is 11. They may, however, be 1-jointed as in *Articerus* or 2-jointed as in many Paussidæ: on the other hand, they may consist of 27 joints or more in rare instances, and there are many transitions between these extremes.

The *mandibles* attain their extreme development in the males of many of the Lucanidæ. In this family they often assume relatively enormous proportions and may be branched in an antler-like manner: in *Chiasognathus* their length exceeds that of the whole body (Fig. 460). In weevils of the genus *Balaninus* they have a vertical movement, side by side, instead of being horizontal and opposed, owing to the dorsal position of their condyles. In the Curculionid sub-families Brachyderinæ and Otiorrhynchinæ each mandible often bears a round or oval area with a raised margin. These structures are the *mandibular scars* which served as supports for the deciduous *provisional mandibles* of the pupa. The latter organs apparently enable the newly emerged imago to cut its way through the cocoon but are cast off soon after the insect has freed itself. In a few genera, however, they are permanently retained. In *Passalus cornutus*, certain Staphylinidæ, Meloidæ, and other beetles a movable inner lobe or *prostheca* is present.

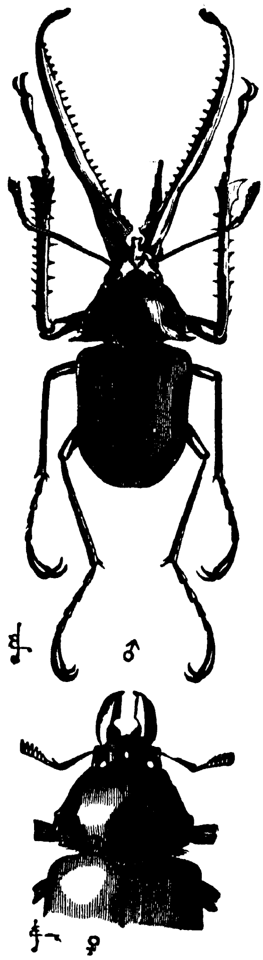

FIG. 460.— *Chiasognathus grantii*, Male and Female.

After Darwin, " Descent of Man."

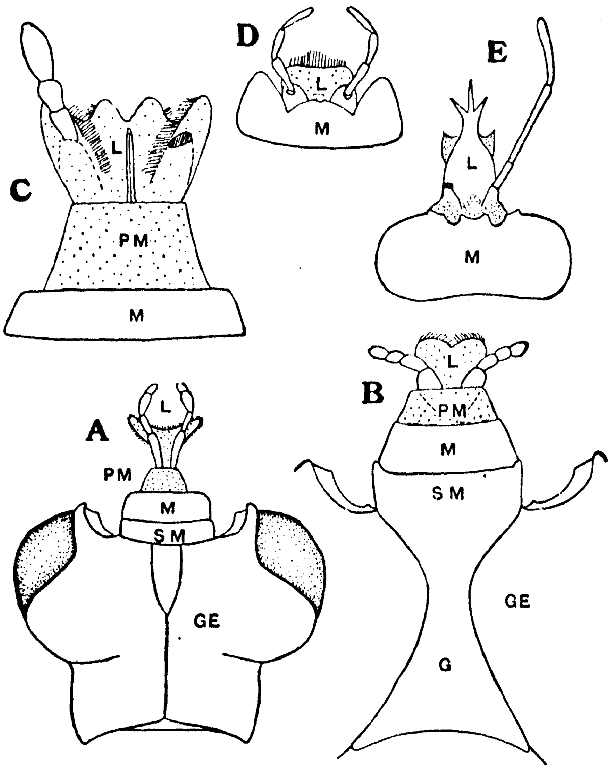

FIG. 461.—*A*, *Necrophorus interruptus*, Ventral Aspect of Head. *B*; *Silpha quadripunctata*, Median Ventral Region of Head. *C*, *Ocypus olens*, Labium. *D*, *Dytiscus marginalis*, Labium. *E*, *Leistus spinibarbis*, Labium.

G, gula; *GE*, gena; *L*, ligula; *M*, mentum; *PM*, prementum; *SM*, submentum.

The *maxillæ*, as a rule, are completely developed with the full number of elements present. In the Adephaga and Dytiscidæ the *galea* is generally 2-jointed and palpiform. The *lacinia* is frequently large and blade-like and may carry an articulated process, well exhibited in the Cicindelidæ where it is claw-like. Specialization by reduction is frequent: thus a single maxillary lobe or *mala* is present, for example, in the Corylophidæ and most of the Nitidulidæ as well as among the Rhynchophora: in other members of the latter group the mala may be wanting. The *maxillary palpi* are generally 4-jointed, and more rarely 3-jointed, while in *Aleochara* they are composed of five joints: in the Pselaphidæ and Hydrophilidæ these organs are very greatly developed.

In the *labium* (Fig. 461) the *mentum* [1] is large and well-developed: the *submentum* is evident in some forms, including *Hydrophilus* and *Necrophorus*, but is usually fused with the gula (Fig. 461, B) or no longer recognizable as an individual sclerite. The *ligula* is extremely variable: in some forms it is entire, in others it presents up to as many as five lobes or processes, apparently of a secondary nature. The *labial palpi* are usually 3-jointed: more rarely, they are 2-jointed, while in certain Staphylinidæ they are unjointed and bristle-like.

The **Thorax.**—The *prothorax* is the largest of the thoracic segments and is usually freely movable, the latter feature being a marked characteristic of the order. The *pronotum* is composed of a single sclerite and is entirely visible from above. The *pleuron* is frequently undivided into sclerites, and the suture between that region and the pronotum, on either side, is likewise often absent: in the latter case a single chitinous shield covers the whole of the dorsal and lateral regions. The pleurosternal sutures are distinct except in the Rhynchophora in which group the whole of the prothoracic sclerites are fused into an undivided annular band. The anterior *coxal cavities* are either entire, when they are

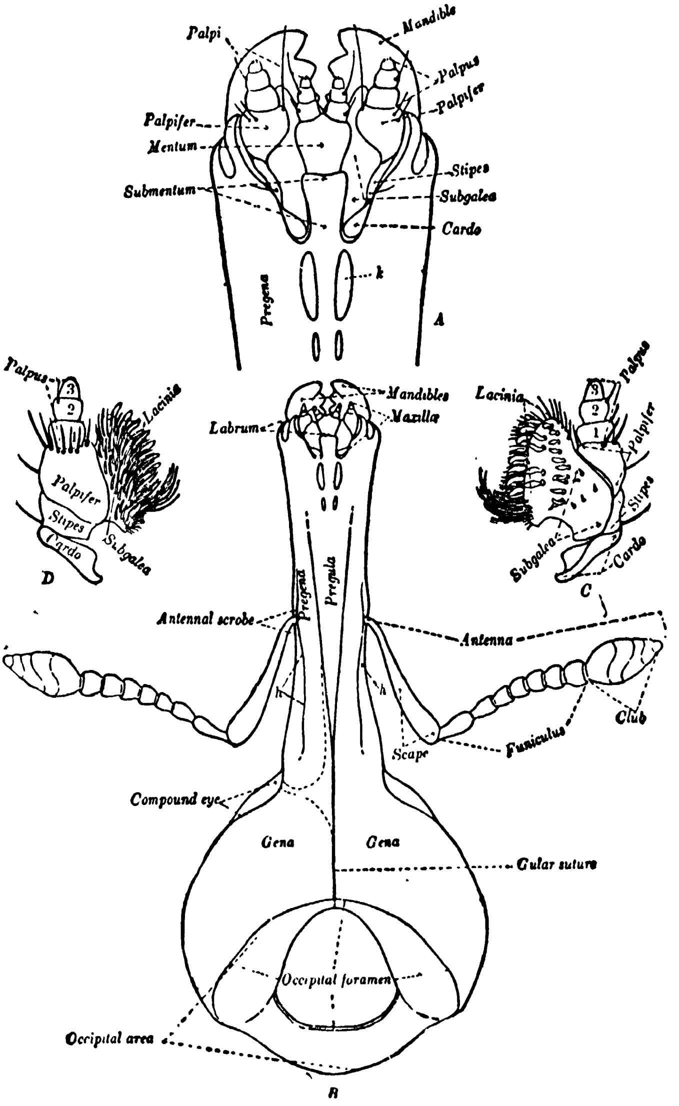

FIG. 462.—*PISSODES STROBI.*

A, ventral aspect of head; *B*, apex of rostrum, ventral; *C*, interno-lateral and *D*, externo-lateral aspects of maxilla. Adapted from Hopkins, *U.S. Dept. Agric. Entom. Tech. Ser.* 20, pt. 1.

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[1] Stickney (1923) and other American morphologists maintain that the principal labial sclerite is the submentum, the mentum being either atrophied or vestigial.

closed behind by the meeting of the prosternum and epimera, or by the meeting of the epimera alone: or they may be open, when the space is only bridged over by the membrane. The *meso-* and *metathorax* are fused together: the former segment is considerably reduced while the latter, on the contrary, is largely developed, except in species in which the wings are absent or non-functional. The tergum of both segments is divisible into *prescutum, scutum* and *scutellum.* The latter sclerite is median in position and divides the scutum into two separated plates. The *metapostnotum* is generally distinct but, according to Snodgrass, the corresponding sclerite of the mesothorax is wanting. With the exception of the *mesoscutellum* the entire dorsal surface of both segments is usually covered by the elytra.

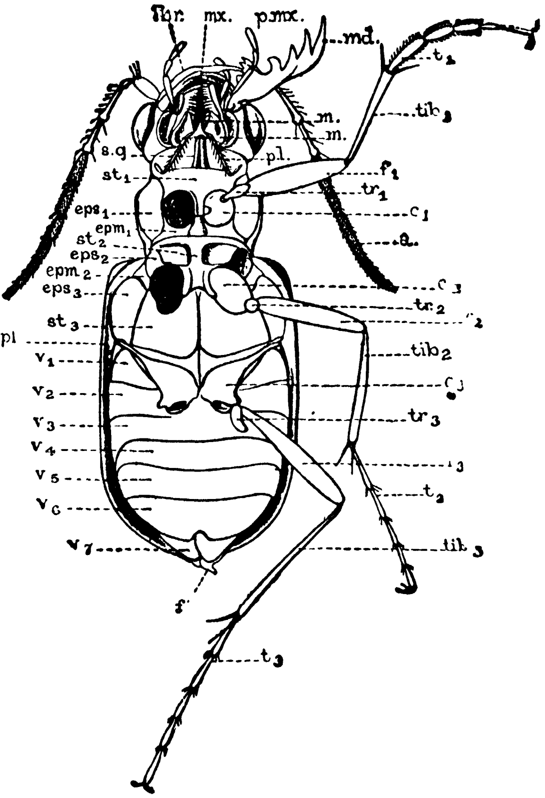

Fig. 463.—*Cicindela*, Ventral Aspect: Male.

lbr, anterior margin of labrum; *md*, mandible; *mx*, maxilla and *p.mx*, palp; *m, m*, mentum; *p.l*, labial palp; *s.g*, gular sutures; st_1-st_3, thoracic sterna; eps_1-eps_3, episterna; epm_1-epm_2, epimera; *epl*, epipleuron; v_1-v_7, abdominal segments; *f*, ædeagus; c_1-c_3, coxae; tr_1-tr_3, trochanters; f_1-f_3, femora; tib_1-tib_3, tibiæ; t_1-t_3, tarsi. Figs. 448 and 449 from Fowler (F.B.I.), *after* Ganglbauer.

The *legs* are generally adapted for walking or running, but in many of the Lamellicornia and certain of the Carabidæ, they are also modified for fossorial purposes. In the Dytiscidæ the hind pair are flattened and used for swimming, while in the Gyrinidæ both the middle and hind pairs are thus modified. In the Halticinæ the hind femora are greatly enlarged for saltatory purposes. The legs of Coleoptera consist of the usual number of joints—and the form and disposition of the coxæ are of great importance in classification. The tarsal joints are extremely variable in number and afford valuable family and superfamily characters. The primitive 5-jointed condition is characteristic of the Adephaga, most Diversicornia and the Lamellicornia. Among the Heteromera the fore and middle tarsi are 5-jointed, and the hind pair 4-jointed. In the Phytophaga and Rhynchophora the fourth and fifth joints are anchylosed, the former being very small. In the Staphylinoidea the joints are very variable in number. Among many of the males of this group, and the Adephaga, one or more of the joints of the anterior tarsi, and sometimes of the middle pair also, are dilated and different from their fellows: this feature attains a high degree of specialization among the Dytiscidæ.

The *elytra* are the highly modified mesothoracic wings and arise simultaneously with the hind-wings: they develop in an exactly similar manner during the greater part of the larval life. In many Carabidæ, Curculionidæ and Ptinidæ the hind-wings are wanting and the elytra are often firmly united so as to be immovable. In Coleoptera capable of flight the elytra

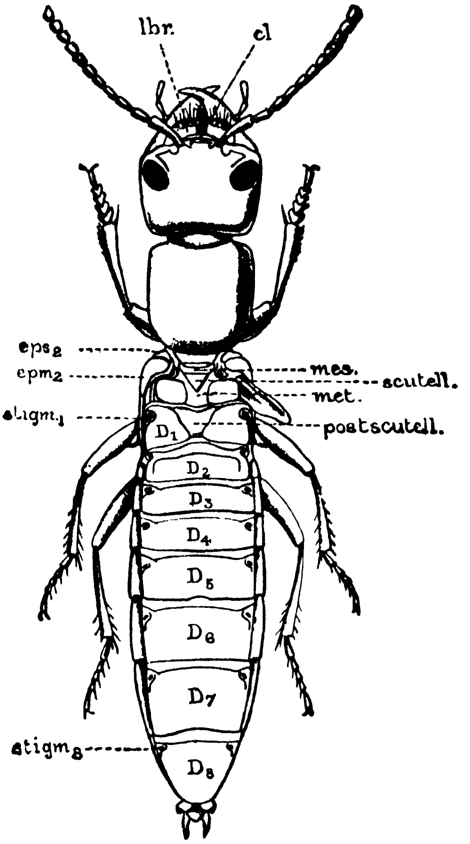

FIG. 464.—*STAPHYLINUS TENEBRICOSUS.* DORSAL ASPECT (ELYTRA REMOVED).

lbr, labrum; *cl*, clypeus; *mes*, mesonotum; *met*, metanotum and *postscutell*, its postscutellum; *stigm*$_1$-*stigm*$_8$, 1st and 8th abdominal spiracles; D_1-D_8, abdominal terga.

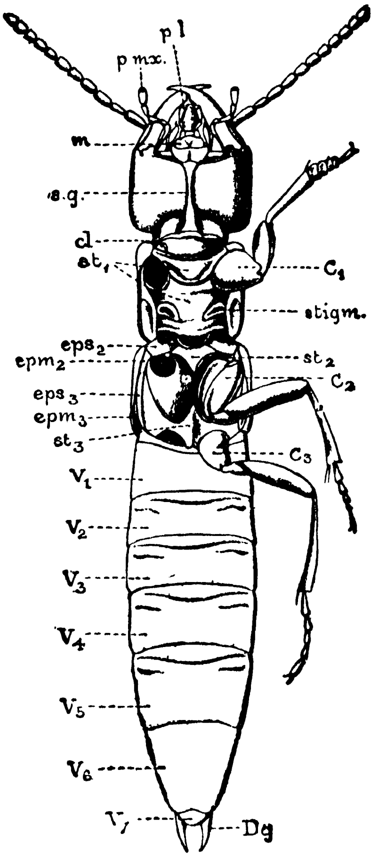

FIG. 465.—VENTRAL ASPECT.

stigm, spiracle on prosternum: *Dg*, anal appendages. Other lettering as in Fig. 463.

are opened to form an angle with the body, and allow of freedom of motion of the wings, but play no direct part in flight. The sides of the elytra are often reflexed to form the *epipleura* (Fig. 463) which conceal the pleura and are well seen, for example, in the Gyrinidæ.

The hard texture of the elytra is due to the thickness of the lower layer of the cuticle, and also to the presence of pillars or trabeculæ which connect the upper and lower elytral surfaces (Fig. 467). The cavity of the elytron is bounded by a thin hypodermis and contains blood, nerves, and tracheæ, often together with numerous groups of gland cells: sometimes small lobules of fat-body are also evident. Comstock states that there is a very close similarity between the tracheation of the elytra and the hind-wings, but in no case yet examined do the principal tracheæ retain the primitive type of branching. The venation of the hind-wings has been studied

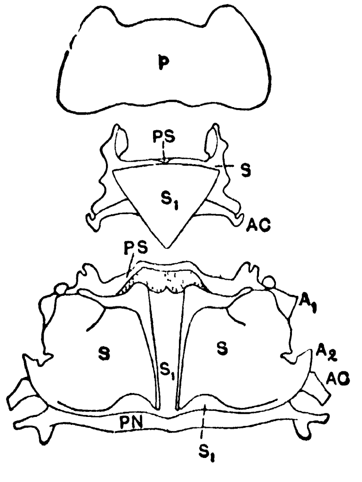

FIG. 466.—*HYDROPHILUS*, DORSAL ASPECT OF THORAX WITH THE SEGMENTS DISARTICULATED.

A_1, anterior wing process; A_2, posterior do.; *AC*, axillary cord; *P*, pronotum; *PN*, postnotum; *PS*, prescutum; *S*, scutum; S_1, scutellum. Partly after Snodgrass, *Proc. U.S. Nat. Mus.* 36.

by Kempers (1909), Kuhne (1915), Orchymont (1921) and Forbes (1922), Figs. 468, 469), and three general types are recognizable. (*a*) *The Adephagid type.*—All the principal veins remain more or less completely developed and are usually joined by a greater number of cross-veins than occur in other Coleoptera. M_1 is connected with M_2 by means of one or two transverse veins: when two are present an oblong cell is formed which is very characteristic of the type. What appears to be the most generalized venation in the order is found in the Cupedidæ. (*b*) *The Staphylinid type.*—Here the chief characteristic is exhibited in the disappearance of all the cross-veins, and the atrophy of the proximal portion of M_1, the remainder of that vein being isolated in the apical portion of the wing. (*c*) *The Cantharid type.*—In this type M_1 and M_2 coalesce distally forming a very definite loop: at the point of junction a single vein (regarded as M_2) is continued to the wing margin. R_2 frequently appears as a recurrent branch of the radius, and cross-veins are commonly present joining the cubital and anal veins. In some cases the M loop is reduced to a mere hook, or may be absent (Passalidæ and many Rhynchophora): when this type of modification occurs, and the cross-veins are atrophied, the Cantharid type is difficult to separate from the Staphylinid one.

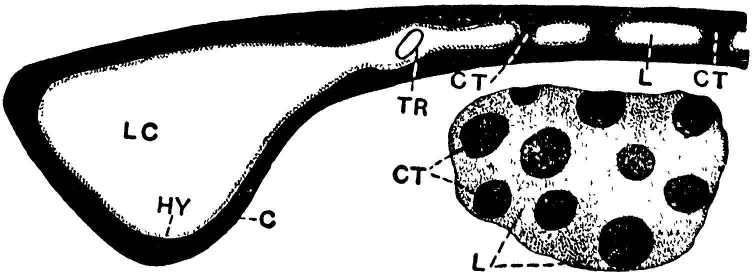

FIG. 467.—TRANSVERSE SECTION OF A PORTION OF AN ELYTRON OF *DYTISCUS* PASSING THROUGH THE OUTER MARGIN: BELOW, A SMALL AREA OF AN ELYTRON SEEN IN SURFACE VIEW (DIAGRAMMATIC).

C, cuticle; *CT*, chitinous trabeculæ; *HY*, hypodermis; *L*, lacunæ; *LC*, lateral blood channel; *TR*, trachea.

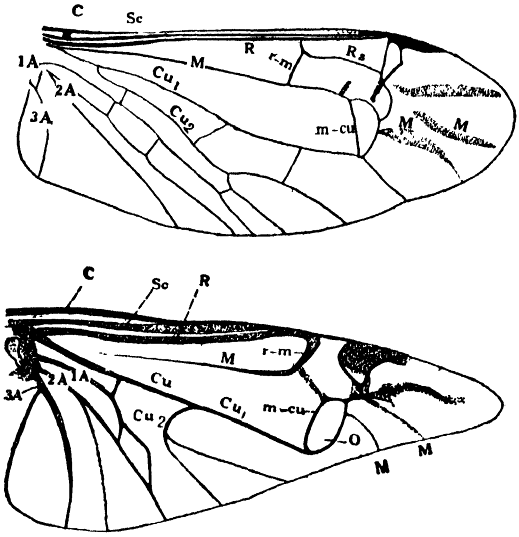

FIG. 468.—ADEPHAGID TYPE OF WING.

Above, Cupedidæ (partly from Forbes). Below, Carabidæ (original). O, Oblong Cell.

The Abdomen.—The number of segments which enter into the composition of this region of the body is difficult to determine. As a rule the first tergum is membranous and one or more of the sterna from the first to the third are aborted. There appears to be at least one sternum generally wanting and with certain exceptions the dorsal and ventral plates do not agree in number. Verhoeff (1893–94) regards the abdomen as consisting of ten segments while Berlese admits a similar number but regards the true first segment as having atrophied, and the last of the series is, on his interpretation, morphologically the eleventh. In most Coleoptera five sterna are visible without dissection but in the Staphylinidæ there are seven or eight. In many cases the terminal abdominal segments of the female are retractile and tubular, thus functioning as an ovipositor. Among the Cerambycidæ, for example, this modification is well exhibited and in certain cases ten terga and nine sterna are recognizable. The male genitalia and associated parts have been studied by Sharp and Muir (1912, 1918) in great detail, who have brought forward a classification of the order founded upon characters afforded by these organs. The genitalia are withdrawn into the abdomen and concealed: they take the form of a tubular evagination, with certain associated sclerites, which arises between the ninth and tenth sterna.

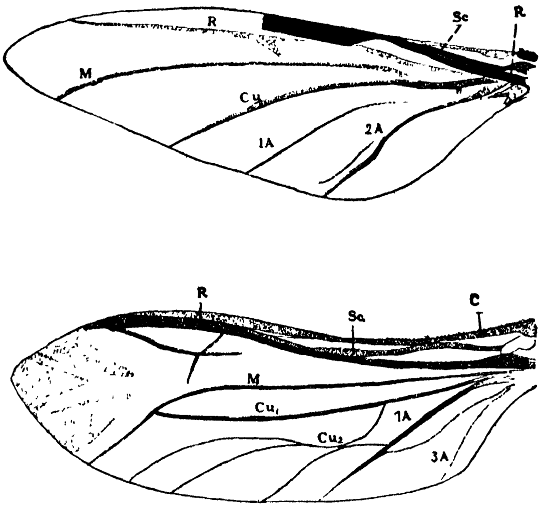

Fig. 469.—Wings of Coleoptera Polyphaga. Above: Staphylinid type (*Ocypus*) Below: Cantharid type (*Cantharis*).

Stridulating Organs.—In one form or another these organs are present in the imagines of a large number of families and have been studied by Darwin ("Descent of Man"), Landois and more recently by Gahan (1900). As the latter author remarks, wherever any part of the exoskeleton is subjected to the friction of an adjoining part by the movements of the insect there, in some species or another, these organs are likely to be found. Their position is not constant, even in different genera of the same family, and they are often similar in structure and location in genera belonging to widely different families. They are most extensively developed in the Lamellicornia where both the larvæ and perfect insects are often capable of stridulation (vide Arrow, 1904). Gahan divides these organs among Coleoptera into four groups according to where they are located, but it is only possible here to refer to one or two examples. In certain Nitidulidæ and Endomychidæ there is a file-like area on the crown of the head which is rasped by the anterior margin of the prothorax In other cases (certain Tenebrionidæ, Scolytidæ, etc.) there is a file-like area on the underside of the head, sound being produced by friction with a projecting ridge on the prosternum. Stridulating organs are found on the mandibles and maxillæ in the larvæ of various Lamellicornia. They are so arranged that a series of teeth on the maxillæ rasp against some granulations on the ventral side of the mandibles, when the maxillæ move forwards and backwards. Many of the Cerambycidæ have stridulatory organs: in some cases the sound is produced by rubbing the hind margin of the prothorax over a striated area of the mesonotum: in others, it is produced by the friction of the hind femora against the edges of the elytra. The most remarkable stridulating organs are those met with in the larvæ of the Lucanidæ, Passalidæ and of *Geotrupes* and its allies. They consist of a series of ridges or tubercles on the middle coxæ, while the hind-legs are modified in various ways as rasping organs. In certain of the Curculionidæ there is a stridulating file on the underside of the elytra near their apices: the rasping is effected by a series of small tubercles situated on the dorsal side of the abdomen. In some cases the file is present on the abdomen in the females, and on the elytra in the males, and the rasping organs are similarly reversed.

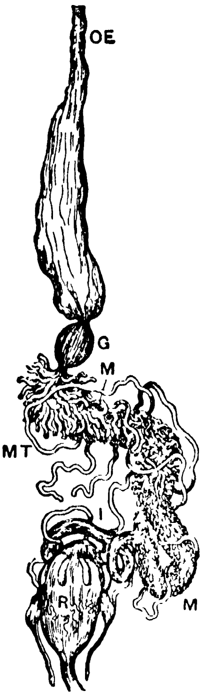

FIG. 470.—*Carabus monilis*, Alimentary Canal.

OE, œsophagus; *G*, gizzard; *M*, mid-intestine; *I*, ileum; *R*, rectum; *MT*, Malpighian tubes. *After* Newport.

Internal Anatomy

The **Digestive System.**—The digestive system of Coleoptera has been mainly studied by Dufour whose results have been published in a series of papers (1824–1840) and Bounoure (1919). Beauregard (1890) has also studied the digestive organs in the Meloidæ, Mingazzini (1889) in the Lamellicornia, Sedlaczek (1902) in the Scolytidæ and Bordas (1903, 1904), in the Hydrophilidæ and Silphidæ. The mouth opens into the *pharynx* or widened commencement of the *œsophagus* and the latter region is a simple tube of variable length. At its hinder extremity the œsophagus expands to form the *crop* which is of very general occurrence although wanting according to Beauregard in pollen-eating beetles such as *Zonitis*, *Sitaris* and *Mylabris*: it is large and capacious in *Carabus* (Fig. 470) and other genera. The œsophagus or crop, as the case may be, is followed by the *gizzard* which is usually a small chamber lined by horny ridges or folds, or with spines or denticles: it is present in many carnivorous and wood-boring Coleoptera, notably in the Cicindelidæ, Carabidæ, Dytiscidæ and Scolytidæ. The *mid-intestine* is very variable in form, and is often of a complex nature. Its most characteristic feature is the presence of large numbers of small villus-like enteric cœca which often vary in character in different portions of the stomach. In the Carabidæ and Dytiscidæ the latter region is a simple slightly tortuous tube provided with numerous closely packed cœca, but the latter are usually wanting from its posterior portion. In *Meloe* the mid-intestine is large and sac-like, occupying the greater part of the abdominal cavity. In the Lamellicornia (Fig. 471) it is very long and convoluted while in *Copris lunaris* it is thrown into a series of numerous coils after the manner of a watch-spring. In the Scolytidæ the mid-intestine is divisible into three regions: a sac-like anterior region, a narrow tubular middle portion and a wider posterior which is partially or completely invested with small cœca. The hind-intestine is always more or less convoluted: it is relatively short in the Cicindelidæ and Carabidæ, but long in *Dytiscus* and many other

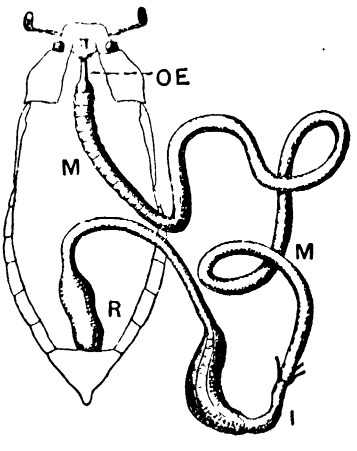

FIG. 471.—*Melolontha vulgaris* Alimentary Canal.

Lettering as in Fig. 454. Adapted from Bounoure.

genera. In the Dytiscidæ (Fig. 472) it gives off a conspicuous *cæcum*, 'an organ which is characteristic of that family (vide Bordas, 1906). Although a relatively small sac in *Ilybius* it attains enormous dimensions in *Dytiscus* and bears an apical tubular appendix: a posterior cœcum is also present in *Silpha* and *Necrophorus*. The *rectum*, when specially differentiated, is often a large chamber: *rectal papillæ* are present in certain Passalidæ and Silphidæ, but as a rule they are wanting.

The *Malpighian tubes* are typically four or six in number and are of considerable importance in the classification of the families into major groups. In the Lampyridæ, where there are four of these vessels, the tubes of each pair unite distally, thus presenting the appearance of loops (Bugnion; *Bull. Soc. Zool. Fr.* 1920). In a number of Coleoptera including *Donacia, Haltica, Cerambyx, Œdemera*, etc., the Malpighian tubes have two apparent terminations in the intestine owing to the fact that their distal extremities become applied to the walls of the colon or rectum, instead of remaining free as in most other insects. In no case, however, have any secondary openings into the hind-intestine been discovered (vide Woods, 1916).

Associated with the alimentary canal are various glands. The *salivary glands* appear to have been very little investigated and they are wanting in many species, but according to Packard they are present in *Anopthalmus*, where there are three pairs, and in *Blaps*: they are also described by Dufour in *Pyrochroa*. *Pygidial glands*, which are defensive in function, exist in many beetles and are very fully discussed by Berlese. They are paired organs secreting corrosive and pungent fluids which can sometimes be ejected to a distance of several inches. These glands open in close association with the anus and, among the Carabidæ, they have been studied in detail by Dierckx (1899) and Bordas (1899). In *Pterostichus vulgaris*, for example, each gland consists of spherical acini composed of gland cells: each acinus opens by a separate duct into the common canal of its side. In *Carabus* and *Cychrus* the ejected fluid contains butyric acid and in *Mormolyce* it is stated to be capable of paralysing the fingers for twenty-four hours afterwards. In *Brachinus* and its allies, and also among the Paussidæ, a volatile vapour is ejected with an audible sound: it is very corrosive and stains the fingers of those who handle these insects. In the Staphylinid genera *Staphylinus, Ocypus, Stenus*, etc., and also in *Lacon* and *Blaps* eversible fœtid anal glands are prevalent.

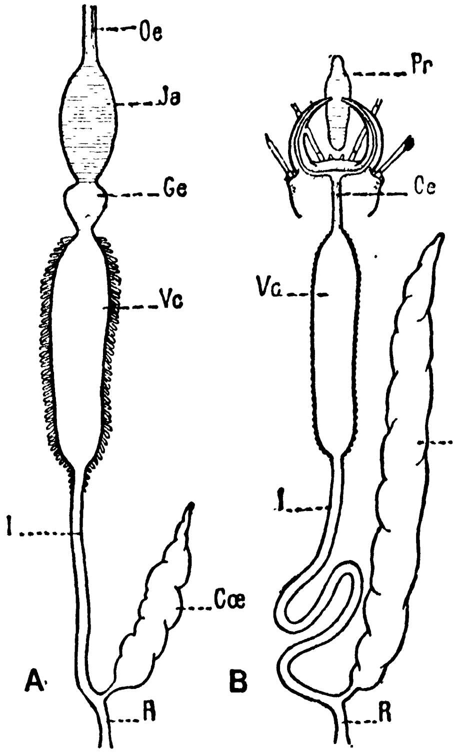

FIG. 472.—*Dytiscus marginalis*; Alimentary Canal of *A*, Imago; and *B*, Larva.

Oe, œsophagus; *Ja*, crop; *Ge*, gizzard; *Vc*, mid-intestine; *I*, hind-intestine; *Cœ*, cœcum; *R*, rectum; *Pr*, prey. *After* Portier.

The **Nervous System.**—The most important differences in the nervous system are exhibited in the ventral cord (vide Brandt, 1879). As a rule the commissures retain their double nature, a feature which is well exhibited in the thorax of most beetles. The most generalized type of nervous system is found in the Cantharidæ where, in addition to the supra- and infra-œsophageal centres, there are three thoracic ganglia and seven or eight abdominal ganglia. The latter number is maintained in *Dictyopterus* and seven abdominal ganglia are found in *Telephorus* and *Lampyris*. Reduction in the number of abdominal ganglia, unaccompanied by a similar specialization of the thoracic centres, may be traced through a number of genera. Thus, in *Cicindela* and *Tenebrio* there are six ganglia in the abdomen; in *Silpha*, *Mordella* and *Creophilus* there are five: in *Donacia*, *Meloe*, and *Callidium* there are four: in *Cassida* there are three and in *Chrysomela* and *Coccinella 7-punctata* there are two. Among the Lamellicornia (*Geotrupes*, *Aphodius*, etc.) the abdominal ganglia are merged into the metathoracic ganglion to form a common centre. In a number of other Coleoptera the meso- and meta-thoracic ganglia are closely united or merged together owing to the disappearance of the connectives between them. This feature is characteristic of many other Lamellicornia (*Melolontha*, *Passalus*, *Lachnosterna*, *Phyllopertha*, *Cetonia*), and the centre thus formed also includes the fused ganglia of the abdominal chain. In the Curculionidæ there are usually two separate abdominal centres, in *Gyrinus* one, and in *Necrophorus* five. The maximum specialization is found in *Sericea brunnea* and *Rhizotrogus solstitialis*. In the former insect all the thoracic and abdominal ganglia unite to form a single complex: in the latter species Brandt states that coalescence has proceeded still further, the infra-œsophageal ganglion being also involved in the fusion.

The **Circulatory System.**—The structure of the dorsal vessel has only been investigated in a few examples. The heart is divided into a variable number of chambers and is continued as the aorta through the thorax into the head where it becomes branched at its apex. In *Melolontha* Straus-Durckheim found nine chambers with eight pairs of ostia. In *Lucanus* Newport described seven chambers and a similar number of pairs of alary muscles.

The **Respiratory System.**—The tracheal system attains its highest degree of differentiation among the actively flying members of the Lamellicornia, particularly in *Geotrupes* and *Melolontha*. Its trunks are greatly ramified and in many species there is an elaborate system of air-sacs. The latter structures do not attain a great size, their chief characteristic being the large numbers present. In *Melolontha* they occur throughout the body, even penetrating into the recesses of the head (vide Straus-Durckheim). In *Lucanus* (male) the large massive head and mandibles are filled with air-sacs, especially the mandibles. Newport states that the air-sacs are developed in rows from long tracheæ which penetrate the jaws, and the latter apparently unwieldy structures are thus rendered extremely light.

As a rule ten pairs of spiracles are present: the first is situated between the pro- and meso thorax and the remaining pairs are metathoracic and abdominal in position. Among the Lamellicornia and certain Rhynchophora and other Coleoptera, the eighth pair of abdominal spiracles is either absent or vestigial and non-functional. In the Scolytidæ the number of functional abdominal spiracles varies from five to seven.

The **Reproductive System.**—The *male reproductive organs* have been investigated by Dufour (1825), Escherich (1894), Bordas (1900), and others. They consist of the testes, the vasa-deferentia, one or more pairs of accessory glands and a median ejaculatory duct. Vesiculæ seminales are often present as dilatations of the vasa deferentia. Two general types of reproductive organs are recognized by Bordas and are based upon characters afforded by the testes (Fig. 473). In the first type these organs are simple and tubular and more or less closely coiled, each being enclosed in a membrane : this type is characteristic of the Adephaga. In the second type the testes are compound and divided into a number of separate follicles. The latter may be rounded capsules, each communicating with the vas deferens by means of a separate duct, as in the Phytophaga, Rhynchophora and Lamellicornia. Or, the testicular follicles may be composed of aggregations of small rounded or oval sessile sacs which open directly into the vas deferens (most other Polyphaga).

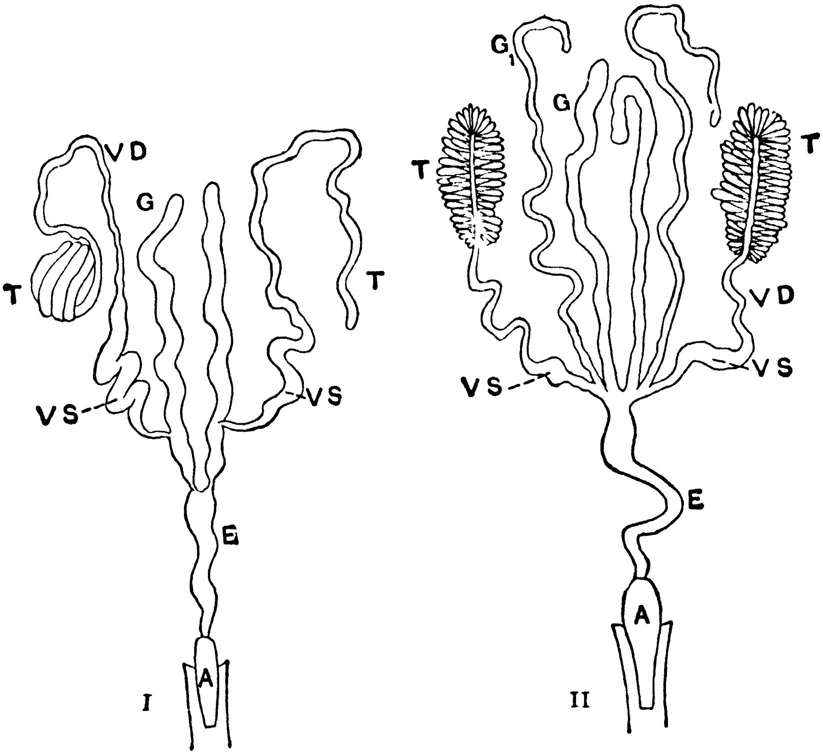

FIG. 473.—MALE REPRODUCTIVE ORGANS OF —I, ADEPHAGA ; II, POLYPHAGA. (The right testis in I is represented uncoiled.)

A, ædeagus ; *E*, ejaculatory duct ; *G*, accessory gland (ectadenes) ; G_1, accessory gland (mesadenes) ; *T*, testis ; *VD*, vas deferens ; *VS*, vesicula seminalis. Adapted from Bordas.

The accessory glands exhibit many differences with regard to their position, number and mode of origin. Escherich (1894) has divided them into ectadenia and mesadenia : the former are believed to arise as ectodermal invaginations of the ejaculatory duct, while the latter are stated to be of mesodermal origin, since they are formed as outgrowths of the vasa deferentia. Definite embryological evidence is needed, however, to substantiate these conclusions.

The *female reproductive organs* (vide Stein) may likewise be divided into two types, according to whether the ovarioles are polytrophic or acrotrophic in character. The former type is characteristic of the Adephaga and the latter type is found, so far as known, throughout the Polyphaga. The ovarioles vary greatly in number : thus in *Ips typographus, Hylobius abietis* and *Sitones lineatus* there are two ovarioles to each ovary : in *Ocypus* *olens* there are three, in certain Elateridæ four, in *Dorcus* and *Saperda carcharias* twelve, in *Byrrhus pilula* there are about twenty, and in the Meloidæ they are extremely short and much more numerous. In some Coleoptera (*Dytiscus*) a colleterial gland is present in association with each oviduct. A *spermatheca* is universally present and opens, by a slender and often exceedingly long duct, either into the vagina or the bursa copulatrix. An accessory gland, of variable character, is generally found in connection with the spermatheca. In many Coleoptera a second passage or "canal of fecundation" leads from the spermatheca or its duct and opens into the vagina near the point of union of the two oviducts (Fig. 474). This canal is believed to allow of the direct passage of the spermatozoa from the spermatheca to the eggs. A *bursa copulatrix* is present as a diverticulum of the wall of the vagina. It is believed that the spermatozoa are received into this sac during copulation and subsequently make their way into the spermatheca. The process of fecundation in Coleoptera, however, is very little understood and the significance of the frequently great length of the spermathecal duct is unknown.

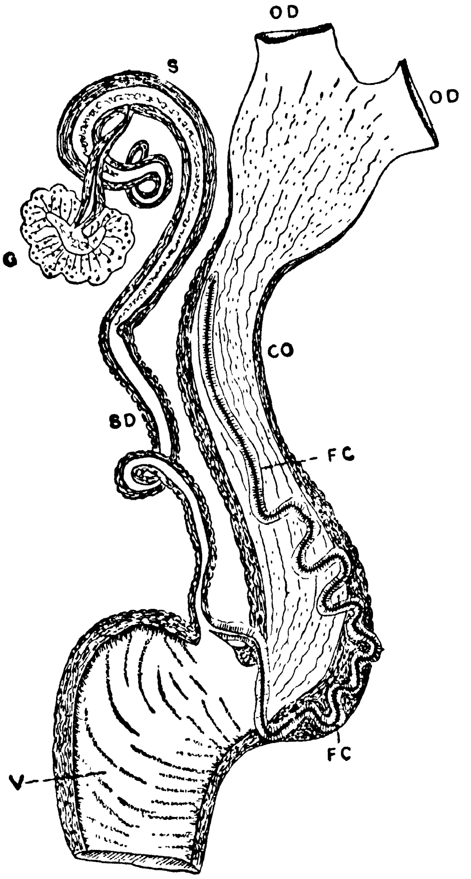

Fig. 474.—*Oodes helopioides* (Carabidæ), Proximal Portion of Female Reproductive Organs.

OD, paired oviduct; *CO*, common oviduct; *S*, spermatheca with *SD* duct and *G* gland; *FC*, fecundation canal; *V*, vagina. *After* Stein.

Metamorphoses

The **Egg.**—The eggs of Coleoptera are usually ovoid in form and rarely exhibit any marked diversity of form or structure as is seen, for example, in the Hemiptera and Lepidoptera. In *Ocypus* they are of unusually large size and few in number, while in the Meloidæ they are small and the number laid by a single female may run into several thousand. Many Coccinellidæ lay their eggs in batches on leaves, the Hydrophilidæ enclose them in cocoons, while among the Cassidinæ they are protected in highly specialized oothecæ. In the Curculionidæ they are frequently deposited in deep holes drilled by the rostum of those beetles in the food-plant. In the Scolytidæ the females have the habit of entering into the trunk or plant within which the eggs are laid.

The **Larva.**—In Coleopterous larvæ the head is well developed, the mouth-parts are adapted for biting and do not differ in their essential features from those of the adults. Such larvæ never possess abdominal feet, but they are generally provided with thoracic legs: cerci may be present or absent. The tracheal system is peripneustic with usually nine pairs of spiracles: the first pair is located, as a rule, between the pro- and mesothorax, and the remaining pairs are situated on the first eight abdominal segments. There is, in many cases, a marked similarity among larvæ of the same family. This is well exhibited for example in the Carabidæ, Buprestidæ and Curculionidæ. On the other hand, the larval differences found among the Chrysomelidæ are scarcely paralleled in any other family of insects. Some of the most remarkable forms occur in the aquatic families Haliplidæ, Gyrinidæ and Hydrophilidæ with their special adaptations to life in the water. Among terrestrial larvæ, those of the Dermestidæ, with their dense clothing of tufted hairs, are totally different in appearance from all other Coleoptera.

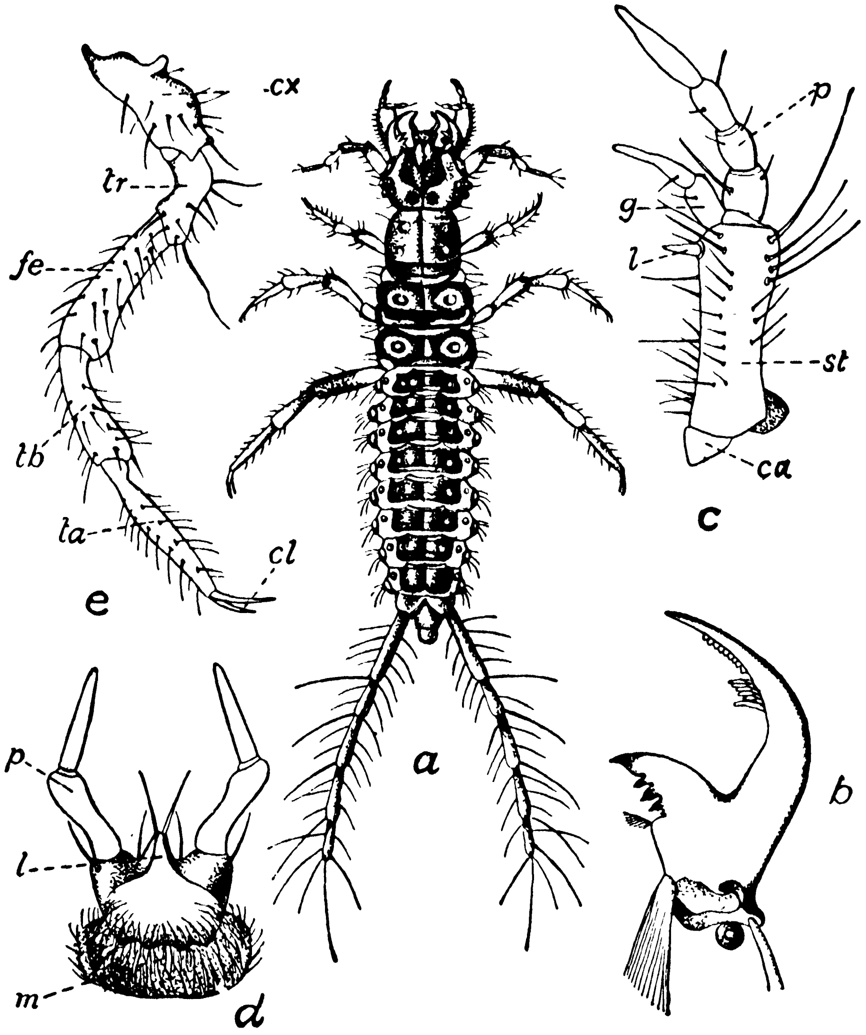

Fig. 475.—*a*, Larva of a Carabid (*Loricera*) × 8. *b*, Mandible × 60; *c*, Maxilla of *Nebria* Larva; *d*, Labium × 32; *e*, Leg of *Nebria* Larva × 24.

From Carpenter *after* Schiödte.

The primitive campodeiform larva (Fig. 475) is characteristic of the Adephaga, many of the Staphylinoidea, and of the first instar in the Meloidæ and Rhipiphoridæ among the Heteromera. Among other of the Staphylinoidea and the vast majority of the Diversicornia and Heteromera, the larvæ are more highly modified and, although they incline to the campodeiform type, they are transitional between the latter and the eruciform type (Fig. 476). Among the Phytophaga, Rhynchophora and Lamellicornia the eruciform larva is prevalent. The extreme apodous type is characteristic of the great majority of the Rhynchophora. It is also met with in certain of the Cerambycidæ and Buprestidæ, in the dung-feeding larva of *Cercyon*, and in the Elaterid sub-family Eucneminæ, while an apodous stage occurs in the ontogeny of members of the Meloidæ and Bruchidæ. It is a comparatively easy matter, therefore, to arrange a graduated series of larval Coleoptera. At the head of such a series is the active, armoured campodeiform type, with well-developed antennæ and mouth-parts, completely formed legs with tarsi and paired claws, and movable jointed cerci: larvæ of this nature are well exhibited in the Carabidæ. At the other extreme are the soft apodous maggots of the Curculionidæ, with their vestigial antennæ, reduced mouth-parts and no cerci. The mode of life is the primary modifying factor in the development of larval types and, once the active predatory habit is lost, structural changes sooner or later supervene and attain their culminating point in the degenerate internal-feeding larvæ that live surrounded by an abundance of nutriment. Hypermetamorphosis is known to occur in a few Coleoptera. It is well exemplified in the Meloidæ whose first instar is a campodeiform larva, and in the later development modified campodeiform, eruciform and apodous stages may be passed through in the ontogeny of an individual species (Fig. 201). Hypermetamorphosis similarly prevails in the Rhipiphoridæ, Micromalthidæ, in *Lebia scapularis* and in the parasitic Staphylinids *Aleochara bilineata* and *algarum*.

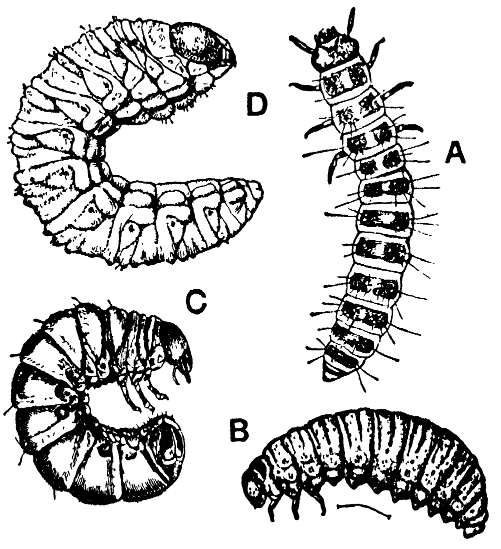

FIG. 476.—COLEOPTEROUS LARVÆ.

A, campodeiform (Cucujidae); *after* Chittenden, *U. S. Ent. Bull.* 4 n.s. B, eruciform (Chrysomelidae); *after* Chittenden, *U. S. Dept. Agric. Year Book*, 1896. C, scarabæiform (Scarabæidæ), *after* Riley. D, eruciform and apodous (Curculionidæ), *after* Chittenden, *U. S. Ent. Bull.* 23 n.s.

The head bears a variable number of ocelli: thus there may be six of these organs on either side as in the Carabidæ and Hydrophilidæ, four in the Cicindelidæ, or they may be reduced to a single one, and even the latter may degenerate into a mere pigment spot. In many larvæ which are internal-feeders ocelli are totally wanting. Antennæ are well developed in campodeiform larvæ, and are very long in those of the Dascillidæ: almost every stage in reduction may be traced until they are represented by single-jointed papilla-like vestiges as in the Curculionidæ. The mandibles are large and exserted in predaceous forms, and in the Dytiscidæ they are specially modified for suctorial purposes. In larvæ which live internally in wood, and other plant-tissues, they are short and stout. Superlinguæ are comparatively well-developed in the Dascillidæ, and vestigial structures of a similar nature occur in the Scarabæidæ (Carpenter and MacDowell, 1912): rudiments have also been found by Mangan in the Dytiscidæ. The maxillæ (Figs. 475, 477) are always well developed: their palpi are variable being long in *Gyrinus* and *Stenus*, while in eruciform larvæ they are often reduced to the condition of 2-jointed papillæ. In the majority of Coleopterous larvæ there is a single lobe or mala which is often composed of two joints. Separately differentiated galeæ and laciniæ are evident, however, in a number of cases and are present, for example, in *Agriotes*, the Byrrhidæ, certain Silphidæ and in the Lamellicornia. The labium is characterized by the absence of paraglossæ : the palpi are commonly 2-jointed but in the Curculionidæ they are represented by single-jointed tubercles. The glossa is frequently present, but is very variable, and in many genera it is not separately distinguishable. In *Silpha* the ligula is represented by a pair of rounded lobes which are perhaps to be regarded as being those of a divided glossa. The legs exhibit different degrees of development : among the Adephaga they are undoubtedly primitive and are characterized by the presence of a distinct tarsal joint and paired claws. These features are lost in the Polyphaga, where the tarsus is not separately differentiated, and the claws are single. Exceptions are extremely few, but in the first instar of the Micromalthidæ and Meloidæ a tarsus is present and the claws are paired. The abdomen is 10-segmented and, among the Carabidæ and Staphylinidæ, the anal segment is often tubular and functions as a pseudopod. Cerci are well developed jointed appendages in many campodeiform larvæ : in other cases they may be fixed and unjointed. The morphology of the rigid horny anal processes of many larvæ is not understood : they have the appearance of being non-appendicular outgrowths of the body-wall, but when their development is studied they may prove, in some cases, to be highly modified cerci.

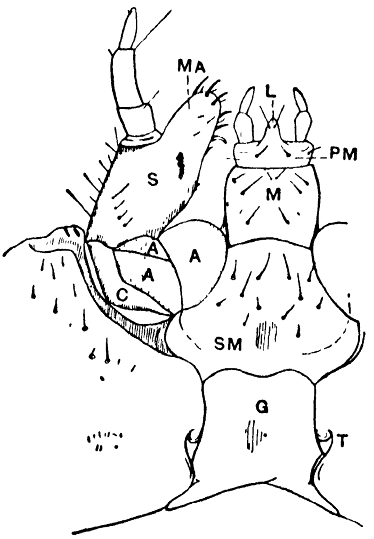

Fig. 477.—Gula, Labium and Right Maxilla of a Tenebrionid Larva (*Embaphion*).

AA, articulating areas ; *C*, cardo ; *G*, gula ; *L*, ligula ; *M*, mentum ; *MA*, mala ; *PM*, prementum ; *S*, stipes ; *SM*, submentum ; *T*, tentorial pit. Adapted from Boving, *Journ. Agric. Res.* 22, 1921.

The respiratory system is subject to comparatively few modifications. The position of the first pair of spiracles is somewhat variable : although commonly intersegmental, they may as in *Telephorus* be located on the mesothorax. Well developed metathoracic spiracles have been observed in the Lycinæ but in other families they are absent or vestigial. The most striking variations occur in aquatic larvæ : *Cnemidotus* and *Gyrinus* are apneustic, and respire by means of filamentous processes of the body-wall, while certain of the Hydrophilidæ are metapneustic.

Information on the internal anatomy of Coleopterous larvæ is fragmentary and very scattered. The alimentary canal has been studied by Portier (1911) in the Dytiscidæ and Hydrophilidæ, by Payne (1916) in *Telephorus*, by Woods (1916, 1918) in *Haltica*, and by Mingazzini (1889) in the Lamellicornia. In the latter group and also in *Telephorus* and *Calosoma* it pursues a straight course from the mouth to the anus, the hind intestine in these instances being short (Fig. 478). In the Dytiscidæ and Scolytidæ the gut is convoluted owing to the increase in length of the hind intestine. A well developed crop is present, for example, in *Calandra* but in *Telephorus*, *Haltica* and *Dendroctonus* it is represented by a small distal enlargement of the œsophagus. A gizzard is present in the latter genus, while both crop and gizzard are wanting in the Dytiscidæ and Hydrophilidæ. The mid-intestine is very variable, but always forms a large portion of the gut, and frequently exhibits differentiation into several distinct regions.

In *Telephorus* it is a large simple sac, but in many larvæ it is coiled and tubular, as for example, in the Dytiscidæ, Hydrophilidæ, and also in *Haltica'* and *Dentroctonus*. Differentiation into separate regions is evidenced by change of calibre, by the histological structure, and the presence or absence of enteric cœca. In *Oryctes*, and other Lamellicornia, the latter structures are very large and are restricted to three annular bands (Fig. 479): in *Calandra* they are represented by numerous papilla-like outgrowths. An extensive cœcum is sometimes present in relation with the hind intestine. In *Dytiscus* it occupies a considerable part of the body cavity and a large cœcum is also present in many Lamellicornia. In the Coprinæ the larvæ have a characteristic dorsal hump which serves for the accommodation of this organ. The Malpighian tubes, as a rule, are similar in number and character to those of the imagines. The nervous system generally consists of three thoracic and seven or eight abdominal ganglia. In *Coccinella 7-punctata* the abdominal ganglia are concentrated in the anterior segments of the hind body, the intervening commissures being very much abbreviated. In *Melolontha*, and other of the Scarabæidæ, the whole of the ventral ganglia are concentrated in the thorax.

The heart has been observed by Payne in *Telephorus*. It is of an extremely narrow calibre and apparently exhibits no division into chambers: nine pairs of alary muscles are present. Segmental glands have been described in a few cases: a pair is present on each of the thoracic and abdominal segments in *Ocypus* (Georgevitsch; *Zool. Anz.* 1898), *Melasoma* (Berlese), and *Telephorus* (Payne).

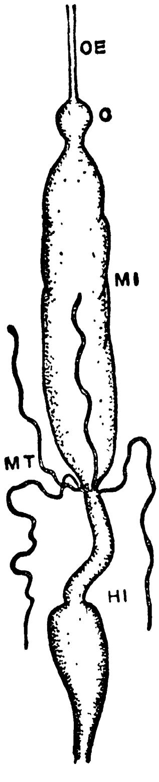

FIG. 478.—*TELEPHORUS*, ALIMENTARY CANAL OF LARVA.

OE, œsophagus; *C*, crop; *MI*, mid-intestine; *MT*, Malpighian tubes; *HI*, hind-intestine.

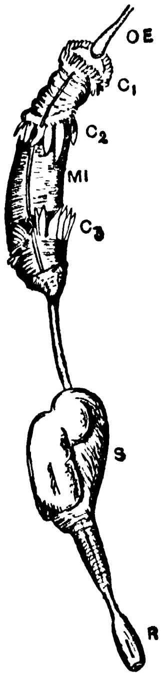

FIG. 479.—*ORYCTES NASICORNIS*, ALIMENTARY CANAL OF LARVA.

OE, œsophagus; C_1C_2-C_3 enteric cœca; *MI*, mid-intestine; *S*, sac of hind-intestine; *R*, rectum. *After* Mingazzini.

The **Pupa**.—The pupæ in this order are of the exarate type, pale-coloured, and are invested by a thin, soft cuticle. In some of the Staphylinidæ they are obtect, being covered by an exudation that solders the appendages down to the body and forms a hardened coat. In the Coccinellidæ the pupæ likewise have a hardened integument and are, moreover, often conspicuously coloured. A large number of Coleoptera pupate in earthen cells below ground: many others pupate within the food plant. A cocoon is frequently present, but the nature and origin of the substance by means of which it is produced needs investigation. In certain of the Curculionidæ the cocoon is formed by a product of the Malpighian tubes, while among several of the Lamellicornia it is described as being formed from the contents of the posterior cœcum. Many of the Cerambycidæ construct pupal cells largely impregnated with carbonate of lime. The naked exposed pupæ of the Coccinellidæ are often protected by the persistent remains of the last larval skin.

Literature on the Metamorphoses.—The most important publications on the life-histories of these insects are those of Schiödte (1862–81), which is written in Latin and has excellent illustrations, and of Böving and Craighead (1931). The complete literature on the transformations of European Coleoptera, up to 1894, has been collated and arranged by Rupertsberger, while Beutenmüller (1891) has catalogued the references to those of the American species : the recent paper by Roberts (1930) should also be consulted. In addition to the above general works, detailed studies of larvæ of several families have been made by Gardner (*Indian Forest Records:* 1926–33).

Classification of Coleoptera

Among the various systems of classification that have been proposed the most satisfactory one yet devised is due to Ganglbauer (1903). The major divisions adopted by this authority take into account a wide range of characters afforded by the external and internal anatomy and the metamorphoses. As an historical study of the classification of the order is desirable to fully grasp the system evolved by Ganglbauer, the student should consult a series of articles by Gahan (1911) or the prefaces to the works of Fowler (1912) or Leng (1920). It is noteworthy that shortly after the publication of his classification Ganglbauer withdrew the family Hydrophilidæ from the Diversicornia to form a separate series—the Palpicornia—but this emendation is not adopted in the present work.

The major divisions of Coleoptera are as follows :—

Sub-order I. ADEPHAGA

Antennæ filiform, rarely moniliform or irregular. Tarsi 5-jointed. Wing venation of Adephagid type. Ovarioles polytrophic, testes simple and tubular with one pair of accessory glands : four Malpighian tubes. Larvæ active, predaceous and carnivorous : campodeiform or only slightly departing from that type : definite tarsi and paired claws usually present.

With a single family series. CARABOIDEA. (p. 495)

Sub-order II. POLYPHAGA

Antennæ and tarsi very variable. Wing venation of the Staphylinid or Cantharid type. Ovarioles acrotrophic : testes follicular with one or more pairs of accessory glands : four or six Malpighian tubes. Larvæ with very variable habits : campodeiform or eruciform ; the legs long or short, almost always without tarsi, and with single claws.

The Polyphaga are divided into the following series :—

1 (2).—Wing venation of the Staphylinid type without cross-veins or loop. Antennæ filiform or clubbed, occasionally irregular. STAPHYLINOIDEA (p. 500)

2 (1).—Wing venation of the Cantharid type, in some forms either so greatly reduced that the type is unrecognizable, or approximating to the Staphylinid type. Antennæ very variable.

3 (9).—Gular sutures and pleuro-sternal sutures of prothorax distinct.

4 (8).—Antennæ without a lamellate club.

5.— Tarsi 1- to 5-jointed, very rarely heteromerous. DIVERSICORNIA (p. 504)

6.— Tarsi heteromerous. HETEROMERA (p. 517)

7.— Tarsi apparently 4-jointed. PHYTOPHAGA (p. 522)

8 (4).—Antennæ with a lamellate club. LAMELLICORNIA (p. 531)

9 (3).—Gular sutures confluent, pleuro-sternal sutures of prothorax atrophied : tarsi as in 7 : head generally prolonged into a rostrum. RHYNCHOPHORA (p. 526)

Sub-order I. ADEPHAGA

Many of the characters of the Adephaga suggest that this sub-order includes the most primitive members of the Coleoptera. The presence of what is morphologically the second abdominal sternum, the usually filiform antennæ, the pentamerous tarsi, the characters afforded by the venation, and the campodeiform larvæ are all suggestive of a primitive origin. According to Gahan (*Ann. Mag. Nat. Hist.*, 5, 1910, p. 57) most of the Adephaga are characterized by the presence of a noto-pleural suture on either side of the prothorax, and it is doubtful whether this suture is ever developed among the Polyphaga. Both larvæ and imagines are predaceous and carnivorous ; a few exceptions are known but exact observations upon the feeding habits are not numerous. The Paussidæ and Rhysodidæ are abnormal in certain features, particularly with regard to their antennal development, and the Gyrinidæ are very highly modified for an aquatic mode of life. *Hydroporus* is exceptional in that the anterior pair of tarsi are 4-jointed.

Key to the families of Adephaga (adapted from Fowler) :—

1 (16).—Six or seven (rarely eight) visible ventral abdominal segments, the first three connate but with the sutures apparent.

2 (11).—Metasternum with a transverse suture before posterior coxæ.

3 (8).—Transverse suture extending across metasternum, the latter continued as an angular process between the posterior coxæ.

4 (7).—Posterior coxæ normal : antennæ 11-jointed.

5 (6).—Clypeus extending laterally before bases of antennæ. CICINDELIDÆ (p. 496)

6 (5).—Clypeus not extending laterally before bases of antennæ. CARABIDÆ (p. 496)

7 (4).—Posterior coxæ very large and plate-like. HALIPLIDÆ (p. 498)

8 (3).—Transverse suture very short, not extending across metasternum, the latter not prolonged between the posterior coxæ.

9 (10).—Anterior coxæ conical, tibiæ and tarsi with swimming hairs. PELOBIIDÆ (p. 497)

10 (9).—Anterior coxæ globular, no swimming hairs. AMPHIZOIDÆ. (p. 497)

11 (2).—Metasternum without a transverse suture before posterior coxæ.

12 (15).—Posterior coxæ contiguous : legs natatorial.

13 (14).—Eyes not divided : antennæ normal. DYTISCIDÆ (p. 498)

14 (13).—Eyes divided : antennæ very short, auriculate. GYRINIDÆ (p. 499)

15 (12).—Posterior coxæ widely separated : legs ambulatorial : antennæ moniliform. RHYSODIDÆ (p. 500)

16 (1).—Abdomen with less than 6 visible ventral segments: antennæ usually more or less abnormal.

17 (18).—Abdomen with 5 visible segments, basal ones connate with no apparent suture: antennæ usually 2-jointed, sometimes 6-11-jointed, nearly always abnormally developed. PAUSSIDÆ (p. 499)

18 (17).—Abdomen with 5 free, ventral segments: antennæ 11-jointed, filiform. CUPEDIDÆ (p. 500)

FAM. CICINDELIDÆ (Tiger Beetles).—The members of this family are among the most voracious and fierce of all insects, particularly in the larval stages and, on account of these habits, they have earned the popular designation of tiger beetles. They are characterized by the markedly prominent eyes, the large and acutely toothed mandibles, and by the lacinia usually terminating in an articulated hook. The legs are long or very long, and there are generally six ventral abdominal segments visible in the female and seven in the male (Fig. 463). The family comprises about 1800 species, the majority being denizens of tropical and subtropical lands. About half its members belong to the genus *Cicindela* and to the latter are assigned the four British representatives of the family. Tiger beetles are often brightly coloured, although they seldom appear conspicuous in their natural surroundings. Their movements are very active, they run with extreme rapidity and many quickly take to the wing. Although their flights are of short duration, their darting movements render it extremely difficult to follow their course with the eye. A large number of the species are most active in hot sunshine but others, including apterous forms, are nocturnal. The species of *Cicindela* chiefly affect open sandy localities, either inland and away from water, or on the sea-shore or along the margins of rivers: *Collyris*, *Tricondyla*, and their allies are largely arboreal.

The larvæ of species of *Cicindela* are described and figured by Schiödte and by V. E. Shelford (*Journ. Linn. Soc. Zool.* 30). They are characterized by the head and prothorax being larger and broader than the rest of the body. The mandibles are large and there are four ocelli on each side. The legs are rather long and slender, the tarsi bear paired claws and there are no anal cerci. The most characteristic organ consists of a pair of hooks arising from a swollen base on the dorsal side of the 5th abdominal segment. These larvæ are ground dwellers, living in burrows which may extend for a foot or more in the earth. The broadened head and prothorax occupy the entrance to the burrow, and its curiously bent body enables the larva to maintain a firm contact with the sides of its abode. This is mainly achieved by the dorsal hooks already mentioned, and the legs also assist in this respect. The food consists of other insects that may wander near the mouth of the burrow and, when the prey is sufficiently near, the larva suddenly throws back its head, seizes the victim with its long sharp jaws, and draws it within the retreat where it is devoured. According to V. E. Shelford the larva of *Cicindela purpurea* requires twelve or thirteen months for its growth and during that time it passes through three ecdyses. The larva of *Neocollyris* has been described by R. Shelford (*Trans. Ent. Soc.*, 1907) and by van Leeuven (*Tijd. Ent.* 1910). It is of the typical Cicindelid form but there is only a single pair of ocelli on each side of the head. In the place of the pair of dorsal abdominal hooks there is a series of three smaller hooks on either side of the same segment. This larva bores into the shoots of tea and coffee plants and, according to van Leeuven, that of *Tricondyla* is very similar in structure and habits.

FAM. CARABIDÆ.—This important family comprises over 24,000 described species and is distributed throughout the world. In temperate regions its members are almost entirely ground beetles occurring in the soil, under stones, in moss and rotting wood, under bark, etc. The elytra in many species are firmly soldered together and the wings are often atrophied. In the tropics there are numerous arboreal genera, with well developed wings and considerable powers of flight. Carabidæ are closely allied to the preceding family but are readily distinguished by the form of the clypeus, and the absence of the terminal hook on the lacinia of the maxilla. In many genera the legs are slender, and adapted for running; in others (*Clivina*, *Dyschirius*, etc.) they are shorter, and are used for digging. Although a considerable number of the species are metallic or otherwise brightly coloured, the majority have the sombre dark coloration of ground insects. Many Carabidæ, in their general configuration, bear a resemblance to the Tenebrionidæ, but may be easily separated upon tarsal characters. Although both the larvæ and adults are essentially carnivorous a few have been recorded as devouring cereals and the seeds of plants, the habit being noted in species of *Harpalus*, *Zabrus*, *Omophron* and *Amara*. *Harpalus ruficornis* sometimes causes damage to strawberries. *Calosoma* largely preys upon lepidopterous larvæ and, of recent years, *C. sycophanta* has been imported in large numbers from Europe into N. America, in order that its predaceous habit may be utilized in destroying the larvæ of the gipsy and brown-tail moths (vide Burgess, *U.S. Bur. Entom. Bull.* 101). Species of *Anophthalmus*, and other genera, are devoid of eyes and live in caverns or beneath huge boulders deeply embedded in the earth. Members of the tribe Brachinina have the property of secreting an evil smelling defensive fluid from the anal end of the body. In the case of the Bombardier beetles (*Brachinus*), this fluid rapidly volatilizes into a gas which appears like a minute jet of smoke when it comes into contact with the air, and its discharge is accompanied by a distinctly audible sound. The fluid possesses caustic properties producing an effect upon the skin resembling that of nitric acid

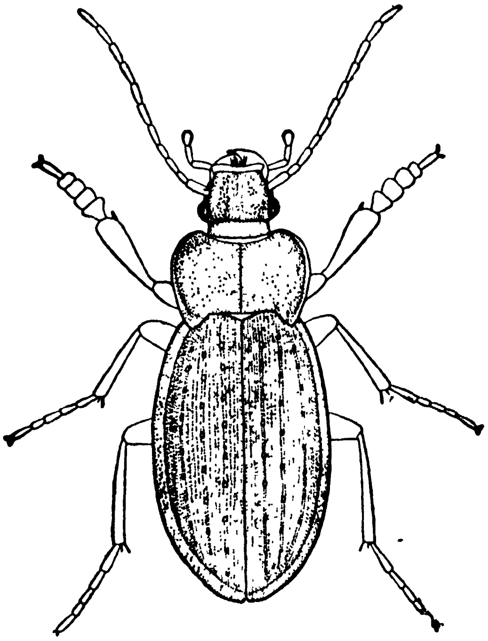

FIG. 480.—*CARABUS NEMORALIS* × $\frac{5}{4}$. EUROPE.

Carabid larvæ (Fig. 481) are very active, linear or elongate in form, with 10 abdominal segments, and the legs are terminated by a pair of claws. The head carries a pair of sharp calliper-like mandibles and there are six ocelli on either side. The 9th abdominal segment carries a pair of cerci of variable length and the 10th segment is tubular in form, and generally provided with a pair of protrusible vesicles (vide Kemner, 1913A). In addition to the writings of Schiödte and Xambeu, a number of Carabid larvæ are described by Boving (*Ent. Medd.* 1910, 1911), Dimmock and Knab (1904), and Kemner (1912, 1913) and the larva of *Pelophila* by Johnson and Carpenter (*Trans. Ent. Soc.*, 1898).

The Carabidæ are divided into four sub-families, the largest being the Harpalinæ with over 10,000 species. The Carabinæ comprise many of the larger and more striking forms (Fig. 480), and the Mormolycinæ include only the Malayan genus *Mormolyce*, in which the lateral borders of the elytra are produced into broad leaf-like expansions. The Pseudomorphinæ are likewise an aberrant group, and have the head grooved on either side for the reception of the antennæ.

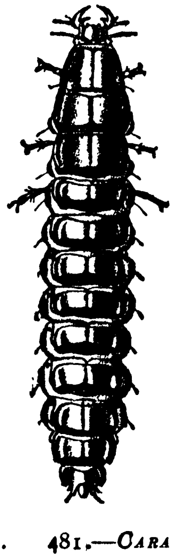

FIG. 481.—*CARABUS CANCELLATUS* LARVA × $\frac{7}{4}$.

From Fowler (F.B.I.) *after* Schiödte.

FAM. AMPHIZOIDÆ.—A very small family consisting of a few species which are indigenous to N. America and Tibet. They frequent cold, rapid streams where they cling to stones and timber, but are not adapted for swimming. The larva of *Amphizoa* is described by Hubbard (*Proc. Ent. Soc. Washington*, 1892): it is likewise aquatic, the side margins of the segments are extended into lamellate prolongations and the larva bears a close resemblance to that of a Silphid. Six ocelli are present on either side, the tarsal claws are paired, and there are eight abdominal segments terminated by a pair of short spine-like cerci. The only pair of functional spiracles are terminal, the remaining pairs being obsolete.

FAM. PELOBIIDÆ (Hygrobiidæ).—Like the Amphizoidæ this is a very small family with a remarkably discontinuous geographical range, its single genus *Pelobius* (*Hygrobia*) occurring in Britain and South Europe, central Asia and Australia. The species are aquatic but, unlike those of *Amphizoa*, the legs are adapted for swimming. *Pelobius tardus* is capable of loud stridulation which is produced by rubbing the apex of the abdomen against a file on the inner aspect of the elytra. The larva of this species is figured by Schiödte; the spiracles are minute and functionless, and it respires by means of a series of ventral branchiæ. The body has a club-shaped appearance owing to the greatly enlarged head and prothorax and the narrow linear abdomen. The latter is terminated by two very long cerci and a median process of very similar proportions. For an account of the biology of this species vide Balfour-Browne (*Proc. Zool. Soc.*, 1922).

FAM. HALIPLIDÆ.—A family of small aquatic beetles of very wide geographical range. They and their larvæ feed upon algæ in both running and standing water, where they are found among aquatic vegetation or under stones. Three genera and rather more than a dozen species are British. Their larvæ are very peculiar and quite distinct from those of any other family of Coleoptera. The whole body is invested by segmentally arranged groups of fleshy process, which are long and thread-like in *Cnemidotus*, and shorter in *Haliplus*. In the latter genus there are eight pairs of abdominal spiracles, but in *Cnemidotus* spiracles are wanting and the processes of the body-wall function as tracheal gills (vide Bertrand, 1928).

FAM. DYTISCIDÆ (True Water Beetles).—Although this family occurs all over the world it is more especially characteristic of the palæarctic region: nearly 2,200 species are known, over 100 being British. Its members frequent both running and standing water, one or two species inhabit thermal springs, while others occur in brackish or more or less salt water. The remarkable eyeless genus *Siettitia* has been found in a deep well fed by a subterranean spring in France. The structure and classification of the family form the subject of a comprehensive memoir by Sharp (1880–82) and this authority points out that, although the Dytiscidæ are aquatic in their larval and imaginal instars, they are to be regarded as modified terrestrial Adephaga. In this connection it may be noted that (1) in their general structure and venation they resemble the Carabidæ, the main differences being in the form of the metasternum, the hind coxæ, and natatorial legs; (2) they drown more quickly than many land beetles do, the imagines can exist perfectly well on land, and are capable of prolonged flight; (3) the pupæ, so far as is known, are terrestrial. These insects may be readily distinguished from the Hydrophilidæ, which they resemble in general shape, by their filiform antennæ: Dytiscidæ are, furthermore, exclusively carnivorous both as larvæ and adults. The hind-legs function as swimming organs, and are greatly flattened, widely separated and fringed with long hairs. In the males of certain genera the first three joints of the fore tarsi are dilated to form highly efficient adhesive pads which are provided beneath with cup-like suckers. The latter are moistened with a glutinous secretion and, according to Blunck (*Zeits. wiss. Zool.*, 1912), this product indirectly aids adhesion after the manner of grease in an air-pump and, directly, by increasing the adhesive force. The male, by the aid of these sucker-pads, is enabled to retain hold of the female for many hours continuously. The best known member of the family is *Dytiscus marginalis*, a species which has been more fully studied from every aspect than any other example of the Coleoptera. The eggs of this insect are laid singly, each in an incision made by the ovipositor in the stem of a water-plant. The larva is extremely voracious and preys upon various aquatic animals including molluscs, worms, insects, tadpoles and even small fishes. The victim is pierced by the long sickle-shaped mandibles which, as Meinert and others have shown, are perforated apically and traversed by a fine canal (Fig. 472). The latter communicates at the base of the mandible with a transverse conduit which, along with its fellow of the opposite side, opens into the pharynx. A secretion of the mid-gut is injected through the mandibles into the prey and digestion of the tissues of the latter takes place externally (vide p 112). By means of the pumping action exerted by the pharynx the liquefied food is imbibed through the mandibular canals and thence into the gut. For details concerning the structure of the mouth-parts and the physiological questions involved vide Portier (1911). In the imago, on the other hand, the mandibles are masticatory and digestion takes place wholly internally. The larva swims with the aid of its legs which are fringed with hairs and are efficient oars: it is also capable of making sudden movements by throwing its body into serpent-like curves. The last two abdominal segments and the small pair of terminal lobes are fringed with hairs, which enable the larva to hang head downwards, suspended from the surface film. In this position it is able to take in air by the caudal pair of spiracles: the remaining seven pairs of the latter organs are rudimentary and closed. When fully fed, the larva makes its way to the moist earth near the water, and there constructs a cell in which pupation takes place. In the adult beetle the last two pairs of spiracles are markedly larger than those preceding. When the insect comes to the surface to breathe the caudal extremity rises above the water, thus placing the enlarged spiracles in communication with the atmosphere. A supply of air, furthermore, is retained beneath the elytra and clings to the felted hairs covering the abdominal terga. This is utilized during submergence and is renewed when the beetle comes to the surface, the elytra being slightly elevated to allow of the free entry of air beneath them.

The literature on *Dytiscus* is very extensive: for further details concerning its structure and biology reference should be made to the great monographic work edited by Korschelt (1923). The larvæ of Dytiscidæ and of the two preceding families are very fully described in the recent memoir by Bertrand (1928).

FAM. GYRINIDÆ (Whirligig Beetles).—Included in this family are about 450 species which are surface swimmers. They are mostly gregarious and sometimes occur in large congregations. Individuals are seen constantly darting in graceful curves around one another with an agility that renders their movements difficult to follow with the eye. The various species are very uniform in appearance, being ovoid or elliptical, more or less flattened, and of a steely-black or bronze lustre. The antennæ are very different from the prevalent Adephagid type, being extremely short and stout, auriculate basally, and inserted beneath the front. The eyes are divided into upper and lower organs, and it has been suggested that the former are adapted for aerial vision and the latter for use beneath the water. The fore-legs are long and prehensile: in the male the tarsi are often dilated and provided with suckers. The hind-legs are broad, greatly flattened, and highly adapted for swimming, while the middle pair are similarly modified, but in a lesser degree. *Gyrinus* is chiefly carnivorous and its eggs are laid end to end in rows upon submerged water plants. The larva (Fig. 482) is elongate with deeply constricted segments, the mandibles are pointed and perforated by a sucking canal, and the legs long with paired claws. Each of the first eight abdominal segments bears a pair of plumose tracheal gills, and two pairs of similar organs are carried on the 9th segment. Pupation takes place in a cocoon which is attached to water plants. *Orectochilus* is the only other British genus and is mainly nocturnal in habits.

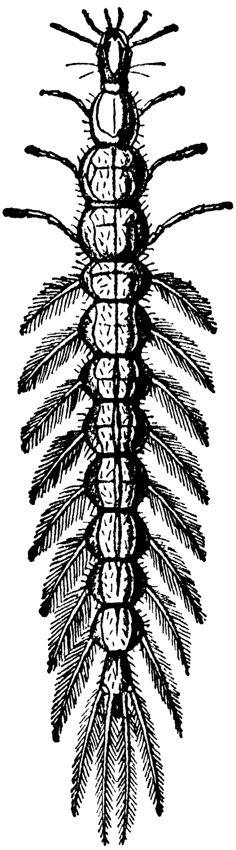

FIG. 482.—*Gyrinus marinus*, Larva × 6.

From Fowler (F.B.I.) *after* Schiödte.

FAM. PAUSSIDÆ.—The Paussidæ include some of the most remarkable of Coleoptera and probably all their species live in some degree of association with ants. They inhabit subtropical and tropical countries, particularly those of the old world; almost all the species are small, and more than 300 are known. They differ from the usual Adephagid type in possessing fewer than six ventral abdominal segments, but the researches of Escherich, Wasmann, and others show that they resemble Carabidæ in certain features of their internal anatomy. Most of the peculiarities which distinguish the Paussidæ from other families are adaptations to a myrmecophilous life, and are most strikingly exhibited in the antennæ (Fig. 483). In *Protopaussus* these appendages retain the simple 11-jointed Carabid type; in *Ceratopterus* and other genera they are 10-jointed and exceedingly broad and compressed; in *Pleuropterus* most of the joints are soldered together and in *Paussus* and many other genera they are 2-jointed. The second joint is greatly enlarged to form a club, which assumes the most bizarre shapes, and is probably developed as the result of the consolidation of an originally multiarticulate flagellum. According to Wasmann (1910) the antennal development is correlated with the growth of a glandular exudatory tissue which produces an aromatic secretion. This tissue is found not only in the enlarged antennal joints but also beneath the body-wall of the head, prothorax and apex of the abdomen. Its positions are indicated by the presence of tufts of yellow hairs or groups of cuticular pores which facilitate the diffusion of its secretion. The latter is eagerly licked by the ants off the bodies of their Paussid inquilines, who are thus enabled to make a return for the hospitality they receive. The metamorphoses of the family have received very little attention: the larva of *Paussus* is of a modified

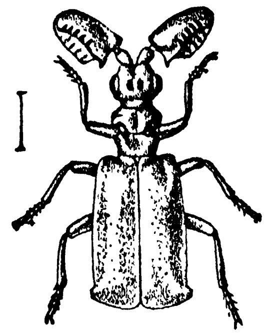

FIG. 483.—*Paussus testaceus*, Tenasserim.

After Fowler (F.B.I.).

Carabid type, and is well described by Boving (*Vidensk. Medd. naturh. Foren., Copenhagen*, 1907).

FAM. RHYSODIDÆ.—The members of this small family are readily distinguished from other Adephaga by their stout and conspicuously moniliform antennæ (Fig. 484). They are linear insects, usually black or dark brown, and somewhat flattened in accordance with a life spent in rotting trees or under bark. The position of the family is doubtful and it appears to have affinities with the Colydidæ and Cucujidæ. Rather more than 100 species have been described and they are widely distributed in both hemispheres. Nothing appears to be known concerning their metamorphoses but their larvæ probably prey upon other lignicolous insects.

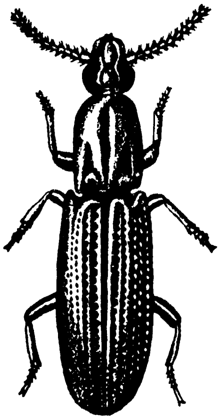

FIG. 484.—*Rhysodes boysi.*
After Fowler (F B.I.).

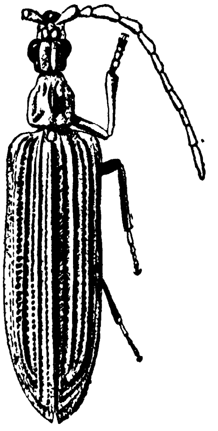

FIG. 485.—*Cupes latreillei.*
After Lameere.

FAM. CUPEDIDÆ (**Cupesidæ** : Fig. 485).—A very small family ranging into both hemispheres, including Australia. Its systematic position is very unsettled and Lameere regarded it as the most primitive family of beetles. The fusion of the 2nd and 3rd abdominal sterna, however, argues against this view, and the family is placed by Sharp with the Cucujidæ. The venation has apparent Adephagid affinities and, as Gahan has pointed out, the presence of noto-pleural sutures on the prothorax suggests a like relationship. The larva of *Cupes*, however, is very different from the Adephagid type (vide Snyder, *Proc. Ent. Soc. Washington*, 1913) and is a wood borer. The body widens somewhat posteriorly and terminates in a stout anal spine; there are no cerci and the legs are short and single-clawed.

Sub-order II. POLYPHAGA

Superfamily I. Staphylinoidea

VENATION OF THE STAPHYLINID TYPE, OFTEN MUCH REDUCED. ANTENNÆ SIMPLE OR CLAVATE, RARELY IRREGULAR. TARSAL JOINTS VARIABLE. TESTICULAR FOLLICLES SESSILE; TWO PAIRS OF MALE ACCESSORY GLANDS; MALPIGHIAN TUBES FOUR. LARVÆ CAMPODEIFORM OR NOT WIDELY DIVERGENT THEREFROM.

The greater number of the species of this superfamily are of small or very small size and it includes the most minute of all Coleoptera. It is only among the Staphylinidæ, Histeridæ and Silphidæ that any considerable proportion of the species attain even a moderate size. The Staphylinoidea exhibit great diversity of habits: the great majority are saprophagous or fungivorous, a smaller number are predaceous upon insects or other animals, several hundreds are denizens of ants' or termites' nests and one or two species are parasites.

The following table (chiefly after Leconte and Horn) will serve as an aid to the recognition of typical members of the various families.

1	(4).—Abdominal segments corneous dorsally: elytra much abbreviated.	
2	(3).—Abdominal segments flexible, 8 visible ventrally: tarsi 3, 4 or 5-jointed.	Staphylinidæ (p. 501)
3	(2).—Abdominal segments connate, 5 or 6 visible ventrally: tarsi with not more than 3 joints.	Pselaphidæ (p. 502)

4 (1).—Abdominal segments membranous dorsally except when exposed at the apex : elytra usually covering or almost covering the abdomen.	
5 (6).—Antennæ geniculate.	Histeridæ (p. 504)
6 (5).—Antennæ not geniculate.	
7 (16).—Legs with at least one pair of tarsi 5-jointed.	
8 (11).—Mentum large, the palpi distant at base.	
9 (10).—Mentum transverse, hind angles prolonged.	Leptinidæ (p. 503)
10 (9).—Mentum prolonged into three obtuse lobes behind.	Platypsyllidæ (p. 503)
11 (8).—Mentum moderate or small, palpi approximated basally.	
12 (13).—Eyes coarsely granulated, posterior coxæ slightly transverse : very small insects.	Scydmænidæ. (p. 502)
13 (12).—Eyes finely granulated, posterior coxæ strongly transverse : size variable.	
14 (15).—Posterior coxæ widely separated.	Scaphidiidæ (p. 504)
15 (16).—Posterior coxæ not widely separated.	Silphidæ : part (p. 502)
16 (7).—Tarsi 3- or 4-jointed.	
17 (22).—Tarsi 3-jointed.	
18 (21).—Abdomen with 6 or 7 sterna.	
19 (20).—Antennæ slender, verticillate, abdomen not prolonged.	Trichopterygidæ (p. 503)
20 (19).—Antennæ short, not verticillate, abdomen prolonged.	Hydroscaphidæ (p. 504)
21 (18).—Abdomen with 3 sterna.	Sphæriidæ (p. 504)
22 (17).—Tarsi 4-jointed.	
23 (24).—Posterior coxæ laminate : insects capable of being more or less contracted into a ball.	Silphidæ (part) (p. 502)
24 (23).—Not as in 23 : third tarsal joint very small.	Corylophidæ (p. 504)

FAM. STAPHYLINIDÆ (Rove Beetles : Figs. 464, 486).—The principal feature of this family is seen in the very short elytra, hence the older name of Brachelytra for the group. Notwithstanding the small size of these organs, they conceal large well developed wings, which are complexly folded away beneath them. On the other hand the unfolding of the wings can take place with great rapidity, thus allowing the insect to resort to almost instantaneous flight. In a few genera (*Olophrum*, *Lathrimæum*, etc.) the elytra are larger than usual, leaving only the apex of the abdomen uncovered. The head is very variable in form and size and frequently differs in the sexes: the antennæ are 10- or 11-jointed and either filiform or more or less clubbed. The eyes are very variable in development though rarely wanting and, in a few cases, a single ocellus or a pair of these organs is also present. The number of joints to the tarsi is inconstant and the latter are sometimes heteromerous. The abdomen is frequently terminated by a pair of styliform appendages, and certain species exhibit the curious habit of curling the distal portion of the hind-body over the back in a threatening manner. The Staphyiinidæ include more than 14,000 species of which over 800 inhabit the British Isles. The majority of species are small and inconspicuous, but a few are brightly coloured and the largest British species, *Ocypus olens* (Fig. 486), attains the exceptional length of 28 mm. Members of the family abound where there is decaying organic matter, including dung and dead animals, while many are predaceous. More than 300 species are known to be mymecophilous (vide p. 593) : thus *Myrmedonia* includes synechrans preying upon dead or disabled ants, while other genera live as tolerated guests of Doryline ants and exhibit a remarkable mimetic resemblance to the latter. *Dinarda* is a synœkete in the nests of certain species of *Formica* and the Aleocharine genera *Lomechusa* and *Atemeles* are highly evolved symphiles which are assiduously tended by ants. Numerous termitophilous genera have been brought to light by Silvestri, Trägårdh and others. Certain of these are viviparous, and *Corotoca*, *Spirachtha*, *Termitomimus* and other genera are physogastric, the abdomen assuming bizarre forms.

Staphylinid larvæ (Fig. 200) are typically campodeiform and often closely resemble those of the Carabidæ. There is no distinct labrum, the body is protected by chitinized segmental scuta and the terminal segment is tubular. The legs have only one claw and cerci are present. The larvæ of certain species are definitely known to be carnivorous and predaceous, a habit which is apparently very general. The larvæ of *Aleochara bilineata* Gyll. and *A. algarum* Fauv. are pupal parasites of cyclorrhaphous Diptera. The life history of the former species has been followed by Wadsworth (*Journ. Econ. Biol.*, 1915). The newly hatched larva is campodeiform and gnaws its way into the puparium of its host. It subsequently undergoes hypermetamorphosis, becoming eruciform, with obvious degeneration in adaptation to a parasitic life. There is, furthermore, strong presumptive evidence that members of other genera are similarly parasites, and they are likely to afford a considerable field for investigation. The degenerate eruciform type of larva also occurs in *Lomechusa* as an adaptation to myrmecophilous habits. The larvæ of *Syntomium* and *Micropeplus* are aberrant, being short and broad and markedly onisciform. A considerable number of Staphylinid larvæ have been described by Kemner, Schiödte and others: for a generic synopsis of the family vide Eichelbaum (1909).

FAM. PSELAPHIDÆ.—A large family of very small reddish or yellow beetles bearing a resemblance to ants. Although worldwide in distribution it attains its greatest development in the tropics. The species mostly live in ants' nests; they present great diversity of form, the antennæ and maxillary palpi being especially remarkable. The Pselaphinæ usually have 11-jointed antennæ and greatly developed maxillary palpi, notably in the males of certain genera. The members of this sub-family are less highly modified than the Clavigerinæ, some are known to be myrmecophilous, while others occur under bark, among moss, etc. The Clavigerinæ are sometimes regarded as a separate family, and are true symphiles. The antennæ are composed of one to six joints and rival those of the Paussidæ in their specialization: the maxillary palpi are greatly reduced or rudimentary and are evidently no longer needed in species which are fed by their hosts. At the base of the abdomen there is an extensive hollow which is surrounded by tufts of golden yellow hair diffusing a substance that the ants are fond of. The European *Claviger testaceus* is well known and lives in the nests of *Lasius*: the ants feed it with regurgitated food and individuals have been kept under observation by Janet for over four years. The chief authority on the Pselaphidæ is Raffray and some of the more remarkable forms are figured in his monograph (*Gen. Insectorum*): rather more than 30 species are British. The larva of *Chennium* resembles the Staphylinid type and is described by Xambeu (*Rev. d'Ent.*, 1889).

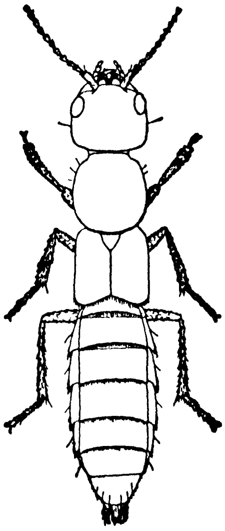

FIG. 486.—*Ocypus olens*, MALE × 2. EUROPE.

FAM. SCYDMÆNIDÆ.—The members of this family are almost all very small insects: they are very widely distributed and more than 1,200 species are known, about two dozen being British. They mostly occur in moss under bark, etc., or in ants' nests, often in company with Pselaphidæ. Although related to the latter family, their 5-jointed tarsi, and longer elytra, afford a ready means of separation. They are more closely allied to the Silphidæ and chiefly differ from the latter in the coarser eye-facets and the separated hind coxæ. The larva of *Scydmænus tarsatus* is figured by Meinert (*Ent. Medd.* I): it is flattened and onisciform in general shape with laterally expanded margins to the segments. Scarcely anything appears to be known of the biology of the family.

FAM. SILPHIDÆ. (Burying and Carrion Beetles).—A large family more especially characteristic of the holarctic region. They exhibit great diversity of form and dimensions, some being extremely minute while others attain a comparatively large size. The antennæ are either clavate, or thickened distally, and the elytra frequently leave the apex of the abdomen exposed. The tarsi are generally 5-jointed, but are variable, and sometimes heteromerous. The various species mostly live on carrion, fungi or decaying vegetable matter, a few are only found in ants' nests, and a number of eyeless species occur in caves. The conspicuous black or black and orange burying beetles (*Necrophorus*) are well known to excavate the ground beneath small dead animals, thereby burying them. They also frequent larger carcasses in considerable numbers. Their eggs are laid in these corpses and their larvæ lead a saprozoic life.

Silpha comprises the roving carrion-beetles (Fig. 487); the larvæ of some species wander in search of decomposing animal matter, those of *S. atrata* and *lævigata* are predaceous upon snails, that of *S. quadripunctata* preys upon lepidopterous larvæ, while the larva of *S. opaca* often attacks beet and other root crops. *Anisotoma* and *Agathidium* comprise a number of small species found among damp herbage, in fungi, under bark, etc. The minute forms constituting the Clambinæ are often regarded as a distinct family: they have the faculty of curling themselves into a ball and the tarsi are 4-jointed. The larvæ of the Silphidæ exhibit great diversity of form: those of several genera are well figured by Schiödte and a table of the described forms is given by Peyerimhoff (*Ann. Soc. Ent. Fr.* 1906). The campodeiform type is exhibited in *Anisotoma*, *Catops* and other genera: the larvæ of *Silpha* are greatly broadened and flattened and bear a resemblance to trilobites: in *Necrophorus* (Fig. 488) they are large yellowish fleshy grubs, with narrow spinose dorsal shields, and reduced anal cerci. The family comprises about 900 species, considerably over 100 being found in the British Isles.

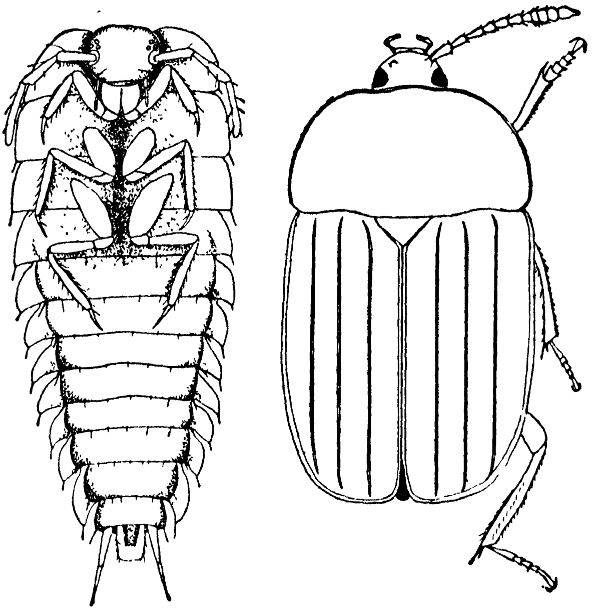

FIG. 487.—*SILPHA TRISTIS*, LARVA AND IMAGO.

FAM. PLATYPSYLLIDÆ.—The single species (*Platypsyllus castoris*) which forms this family is one of the most aberrant of the Coleoptera. It has been found on the beaver in Europe and America but whether it preys upon ectoparasites of that animal, or feeds upon cutaneous substances only, is unknown. The head is provided with a comb-like row of spines near the hind margin, eyes are wanting and the mandibles are vestigial. The maxillæ, however, are well developed and not unlike those of other Coleoptera. The elytra are short, leaving six abdominal segments exposed, and there are no wings. The relationships of this curious insect have been much discussed, and it has been regarded as constituting a separate order. The larva, however, is undoubtedly coleopterous; it is well figured by Bugnion and du Buysson (*Ann. Sci. Nat. Zool.* 10 Ser., t. 7, 1924) who also discuss the affinities of the family.

FAM. LEPTINIDÆ.—This very small family is closely allied to the Silphidæ; the antennæ are long and filiform and the eyes are vestigial or absent. *Leptinus testaceus* occurs in Britain and is holarctic in its range. Its habits are unknown but it has been found in rotten wood, in the nests of birds and field mice as well as in those of *Bombus* and *Formica*. *Leptinellus* is stated by Riley to live on the beaver in company with *Platypsyllus*, and its structure is described by Bugnion and du Buysson (*loc. cit.*).

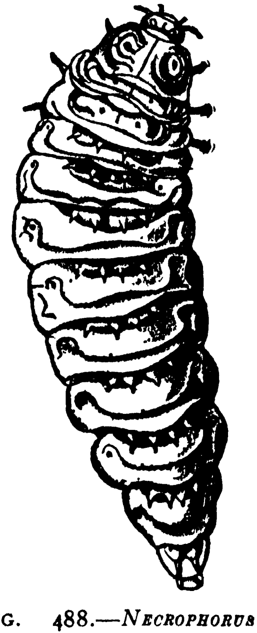

FIG. 488.—*NECROPHORUS VESPILLO*, LARVA × 3. From Fowler (F.B.I.) *after* Schiödte.

FAM. TRICHOPTERYGIDÆ.—All the members of this family are exceedingly minute: the neotropical *Nanosella fungi* is stated to be the smallest known Coleopteron and measures ·25 mm. long, while the maximum size in any species is only about 2 mm. The elytra are variable in length and the wings are very narrow, with a marginal fringe of exceptionally long hairs. These insects abound in decaying vegetable matter of various kinds, in fungi, and under bark. The larvæ are figured by Perris (1876) and by Matthews. The family is probably nearly world-wide and about 80 species are found in England (vide Matthews, 1872).

FAM. HYDROSCAPHIDÆ.—These very minute insects are Trichopterygidæ adapted for an aquatic life (Fowler). They occur in running water, including hot springs, and the larva of *Hydroscapha* is well figured by Boving (*Proc. Ent. Soc. Washington,* 16). According to this observer its structure shows that the genus must be referred to the Hydrophilidæ. It is apneustic and respiration is stated to take place by means of three pairs of jointed processes. Only four or five species, from Southern Europe, India and N. America, are known.

FAM. SPHÆRIIDÆ.—A small family consisting of about half a dozen minute species of which *Sphærius acaroides* occurs in the English fen district.

FAM. CORYLOPHIDÆ.—The species of this family mostly occur in rotting wood or decaying vegetation. They are all very small, the wings are fringed with long hairs and the tarsi apparently 3-jointed, the third joint being minute and concealed by the second. The larvæ of *Orthoperus* and *Arthrolips* are figured by Perris. This family, together with the Sphæriidæ, has been monographed by Matthews (1899). *Aphanocephalus* is an anomalous genus and has been separated to form the family Pseudocorylophidæ.

FAM. SCAPHIDIIDÆ.—The members of this family are fungivorous or occur in rotting wood both as larvæ and adults. They are small, oval, convex and very shining insects with filiform or slightly clavate antennæ. Their affinities have been much disputed, some authorities placing the family in the Diversicornia. Only about 300 species are known, and the few British representatives belong to the genera *Scaphidium* and *Scaphistoma.* The larva of the last-mentioned genus is described by Perris: it is of a modified campodeiform type with elongate hairs along the sides, rather long antennæ, and greatly reduced cerci.

FAM. HISTERIDÆ.—The Histeridæ are a large family of compact hard, shining beetles with geniculate and strongly clubbed antennæ. The elytra are truncated behind leaving the two apical segments exposed. For the most part they are black or brown insects, but in some cases the elytra are marked with red, and a few species are metallic. When alarmed they simulate death and closely retract the antennæ and legs beneath the body. *Hister* (Fig. 489) frequents dung and carrion: *Hololepta* and *Platysoma* live beneath bark and are greatly flattened: others are cylindrical and live in the burrows of wood-boring insects. Several genera are found in ants' nests and others in those of termites. The larvæ have a soft and often much wrinkled integument, very short legs and no ocelli or labrum. The mandibles and palpi are prominent, while the broad 9th abdominal segment bears short 2-jointed cerci. So far as known they are carnivorous; the larva of *Saprinus virescens* preys upon that of *Phædon, Hister pustulosus* attacks *Agrotid* larvæ, while the dung-feeding and lignicolous forms probably prey upon dipterous and other larvæ. The genus *Niponius* is chiefly characterized by the very large head and slender tarsi: its larva frequents the burrows of Scolytidæ and probably preys upon the immature stages of the latter. *Niponius* occurs in Japan, the Himalaya and Borneo, and has been regarded as representing a separate family: for its larva, see Gardner (*Bull. Ent. Res.* 21, 1930).

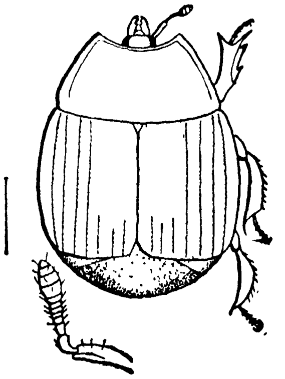

FIG. 489.—*Hister unicolor* Europe.

In addition to the foregoing, the Phænocephalidæ are a very small family containing a single genus which occurs in Japan.

Superfamily II. **Diversicornia**

VENATION OF THE CANTHARID TYPE OR APPROXIMATING TO THE STAPHYLINID TYPE, SOMETIMES GREATLY REDUCED. ANTENNÆ VERY VARIABLE. TARSI 1 TO 5-JOINTED, ONLY EXCEPTIONALLY HETEROMEROUS. TESTICULAR FOLLICLES SESSILE: TWO OR THREE PAIRS OF MALE ACCESSORY GLANDS: FOUR OR SIX MALPIGHIAN TUBES. LARVÆ SOMETIMES CAMPODEIFORM, MORE OFTEN OF AN INTERMEDIATE TYPE OR ERUCIFORM: IN SOME CASES APODOUS.

Included in this superfamily are the series Clavicornia and Serricornia of many authorities. These two groups are very closely connected by transitional forms rendering their exact definition impossible. To give any tabular synopsis of the families of the world is a matter of great difficulty. Their affinities are so intermingled, and exceptions are so numerous, that only a very cumbrous and highly involved synopsis is possible at all. The attempts that have been made mostly have only a limited application and are often misleading. The student is, therefore, advised to become thoroughly acquainted with the structure of the more easily recognizable families in the first instance, and gradually identify the remainder with the aid of a reference collection. In drawing up the family characters free use has been made of the works of Sharp and Fowler. The following families (pp. 505-511) are regarded as constituting the old series Clavicornia which usually have clubbed antennæ: their order of arrangement is entirely provisional. For the larvæ of many of the families see Verhoeff (1922).

FAM. SYNTELIIDÆ.—ANTENNÆ STRONGLY CLUBBED. FORE AND HIND COXÆ TRANSVERSE, CONTIGUOUS. ABDOMINAL SEGMENTS CORNEOUS, APEX OF ABDOMEN NOT COVERED BY ELYTRA. A very small family related to the Histeridæ and Silphidæ. *Syntelia* (Fig. 490) occurs in Mexico and the Orient where it has been found at the sap exuding from wounded trees. The **SPHÆRITIDÆ** are closely allied to the above and are represented by *Sphærites*: *S. glabratus* is found in decaying organic matter and, though rare in Britain, is widely distributed in the holarctic region.

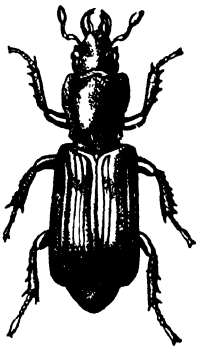

FIG. 490.—*SYNTELIA INDICA*.

After Fowler (F.B.I.).

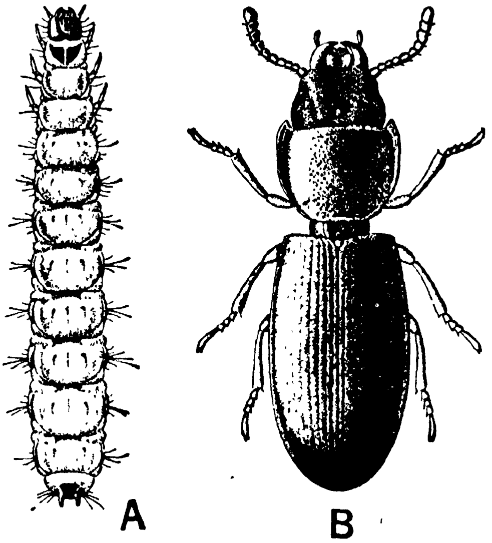

FIG. 491. — *TENEBRIOIDES MAURITANICUS*. A, LARVA ; B, IMAGO. ENLARGED.

After Fletcher and Ghosh. *Proc* 3rd *Ent. Meeting, Pusa.* 1919.

FAM. TROGOSITIDÆ. — CLOSELY ALLIED TO THE NITIDULIDÆ, BUT WITH THE 1ST TARSAL JOINT VERY SMALL AND THE 5TH NORMAL : HIND COXÆ CONTIGUOUS. The majority of species of this family are tropical, only three genera and as many species being British. They vary greatly in form, some being elongate and cylindrical, others almost hemispherical. Several genera inhabit decaying trees, and prey upon the larvæ of other lignicolous insects, while others occur in fungi. The cosmopolitan "Cadelle" *Tenebrioides mauritanicus* (Fig. 491) is found in flour, grain and many other stored products : it is often injurious but the damage it causes is to some extent counterbalanced by its also being predaceous. Its whitish cylindrical larva is furnished with long setæ along the sides and the thoracic terga are protected by chitinized shields : the last abdominal segment is brown-black and bears two strong spines. The larva of *Nemosoma* is described by Erichson (*Naturg. Ins. Deutsch.*, 3) : that of *Thymalus* by Chapius and Candèze and the larva of *Temnochila* by Perris.

FAM. HELOTIDÆ.—ANTERIOR AND MIDDLE COXAL CAVITIES ROUND, ALL THE COXÆ WIDELY SEPARATED. ABDOMEN WITH FIVE VISIBLE VENTRAL SEGMENTS, ALL MOBILE. The members of this family are closely allied to the Trogositidæ and Nitidulidæ : the shape of the coxal cavities and the presence of two raised waxy spots on each elytron serve to distinguish them. About 40 species are known from the Oriental region and Japan. They have been observed by Lewis feeding on the exuding sap of trees.

FAM. BYTURIDÆ.—ANTENNÆ 11-JOINTED, INSERTED BEFORE THE EYES.

ANTERIOR COXAL CAVITIES CLOSED BEHIND, MESEPIMERA REACHING MIDDLE COXAL CAVITIES. TARSI 5-JOINTED, 2ND AND 3RD JOINTS LOBED BENEATH, 4TH JOINT SMALL: CLAWS TOOTHED. This small family is constituted by the genus *Byturus* and includes a few small pubescent species infesting the raspberry and allied plants. The adults often cause great injury to the blossoms and the larvæ are destructive to the fruit: for the biology of *Byturus tomentosus* vide Theobald (*Ins. Pests of Fruit*). The position of the family is doubtful and Sharp relegates it to the Dermestidæ.

FAM. NITIDULIDÆ.—MOSTLY SMALL INSECTS OFTEN WITH AT LEAST ONE OR TWO ABDOMINAL SEGMENTS UNCOVERED BY THE ELYTRA. ALL THE COXÆ SEPARATED AND EACH WITH AN EXTERNAL PROLONGATION. TARSI USUALLY 5-JOINTED, THE 4TH JOINT SMALLEST. ABDOMEN WITH FIVE VISIBLE SEGMENTS. A large family of about 2,200 species which are extremely variable in form, structure and habits (Fig. 492). Several genera with abbreviated elytra very closely resemble Staphylinidæ. A large number inhabit flowers and, in some cases, are restricted to particular species of the latter: others are found in fungi or in decaying animal matter: *Carpophilus* occurs in dried fruits, grain, etc., while *Glischrochilus* (*Ips*) and *Rhizophagus* are found under bark or at exuding sap. The two latter genera connect this family with the Trogositidæ. The larvæ of various Nitidulidæ have been studied by Perris. Those of certain species of *Meligethes* are sometimes injurious to cultivated Cruciferæ while the larvæ of *Glischrochilus* and *Rhizophagus* are predaceous upon *Hylurgus*, *Hylobius* and other xylophagous Coleoptera.

FAM. CUCUJIDÆ.—USUALLY FLATTENED INSECTS WITH THE ANTENNÆ OFTEN SIMPLE BUT SOMETIMES DISTALLY ENLARGED. TARSI 4- OR 5-JOINTED, SOMETIMES HETEROMEROUS IN THE MALES, FIRST JOINT OFTEN SHORT. FORE AND MIDDLE COXÆ GLOBULAR BUT WITH AN ANGULAR EXTERNAL PROLONGATION. ABDOMEN WITH FIVE MOVABLE SEGMENTS EVIDENT VENTRALLY. This family is difficult to define and includes a great diversity of forms, mostly living beneath bark or in the borings of xylophagous insects. Nearly 500 species are known, about a score being British. Wheeler (*Zoologica*, 1921) has discovered in British Guiana two semi-social species (*Coccidotrophus socialis* and *Eunausibius Wheeleri*) which live, along with their brood, in the hollow leaf-petioles of *Tachigalia paniculata*. They are accompanied by a coccid (*Pseudococcus bromeliæ*) whose honey-dew is solicited by the beetles and their larvæ. Cucujid larvæ (vide Perris) differ greatly in form, some being flattened and others more convex and cylindrical: the body is usually terminated by a pair of slender cerci, but in *Læmophlœus* there are a pair of hooks, and in *Silvanus* the last segment is simple. Many of the larvæ are predaceous upon lignicolous insects but a certain number occur in rice, sugar, grain, lac, etc. Several of the species, notably *Silvanus surinamensis*, affecting stoed products, have become widely distributed through commerce. For a bibliograrphy of the described larvæ of the family vide Gravely (*Rec. Ind. Mus.* 11).

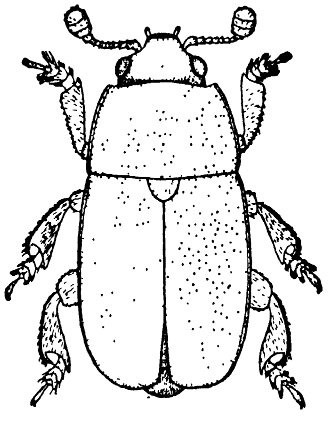

FIG. 492.—*MELIGETHES ÆNEUS* EUROPE. × 22.

FAM. MONOTOMIDÆ.—ALLIED TO THE CUCUJIDÆ BUT DIFFERING IN POSSESSING APPARENTLY 3-JOINTED TARSI, IN THE EXPOSED PYGIDIUM AND IN THE 1ST AND 5TH ABDOMINAL STERNA BEING LONGER THAN THE OTHERS. A widely distributed family consisting for the most part of very small insects found under bark, among vegetable refuse, etc. *Monotoma* is represented by nine species in the British Isles.

FAM. EROTYLIDÆ.—ANTENNÆ STRONGLY CLUBBED. FORE AND MIDDLE COXÆ GLOBOSE: TARSI 5-JOINTED, THE FOURTH JOINT USUALLY MINUTE, THE FIRST THREE MORE OR LESS BROAD AND PUBESCENT BENEATH. ELYTRA ENTIRELY COVERING ABDOMEN WHICH IS COMPOSED OF FIVE VISIBLE STERNA. A large family principally inhabiting fungi and timber and mainly tropical in its distribution. The Dacninæ show relationships with the next family and the Langurinæ resemble the Phytophaga in some respects. The last-mentioned sub-family are very like Elateridæ in general form: their larvæ have been found in herbaceous plants and many of the beetles have a well developed stridulating organ on the head. The Erotylidæ are represented in the British Isles by six species.

FAM. CRYPTOPHAGIDÆ.—SMALL INSECTS, MORE OR LESS ELONGATE. FORE AND MIDDLE COXÆ VERY SMALL: TARSI 5-JOINTED OR SOMETIMES HETEROMEROUS IN THE MALES. ELYTRA COVERING ABDOMEN AND MORE OR LESS SETOSE OR PUBESCENT.

ABDOMEN WITH FIVE VISIBLE STERNA, THE FIRST BEING THE LONGEST. The two principal British genera are *Cryptophagus* and *Atomaria* (Fig. 493) both of which are represented by numerous species. The members of the family vary in habits, some being found under bark or in fungi, others in flowers or about water plants: a few occur in wasps' and ants' nests and many among decaying organic matter of various kinds. The family is closely related to the Erotylidæ and is regarded by Ganglbauer as a subdivision of the latter. The **CATOPROCHOTIDÆ** may be mentioned here: they consist of a few small species found in Turkestan.

FAM. PHALACRIDÆ.—SMALL OVAL AND COMPACT, SHINY, CONVEX INSECTS WITH 5-JOINTED TARSI, THE FOURTH JOINT MINUTE OR VESTIGIAL. ANTERIOR COXÆ GLOBULAR, POSTERIOR CONTIGUOUS. These obscure insects mostly live in flowers, particularly fruit blossoms and the capitula of Compositæ. According to Hegeer (*S. B. Ak. Wien.*, 24) the larvæ of *Olibrus* bore into stems and pupate below ground: in favourable seasons he has observed six generations in the year. The family is represented in most parts of the world and there are about 15 species in Britain. For the habits and larva of *Phalacrus corruscus* vide Friederichs (*Arb. Biol. Anst. Berlin*, 6). The **THORICTIDÆ** are a small family of myrmecophilous beetles almost confined to the Mediterranean region: the thorax is supplied with tufts of golden hairs which, according to Wasmann, diffuse a secretion attractive to ants. The **DERODONTIDÆ** are of doubtful position and include a few little known species occurring in parts of Europe, N. America and Japan.

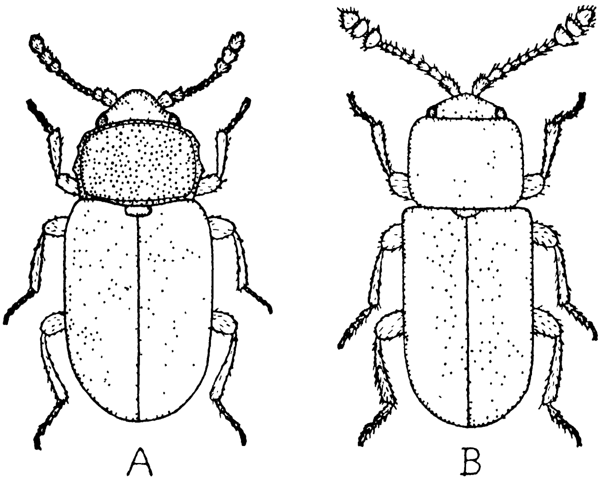

FIG. 493.—A, *Cryptophagus dentatus*. × 20. B, *Atomaria linearis*. × 35.

FAM. LATHRIDIIDÆ.—MINUTE INSECTS WITH 3-JOINTED TARSI AND THE ANTERIOR COXÆ GLOBULAR OR CONICAL. ABDOMEN WITH FIVE OR SIX MOBILE STERNA OF NEARLY EQUAL LENGTH, AND COVERED BY THE ELYTRA. The members of this family amount to about 700 species found in moss, decaying wood and other vegetable matter and fungi: a few have occurred in herbaria, dried carcasses and in ants' nests. Nearly 40 species occur in Britain: some are almost cosmopolitan and *Lathridius nodifer* though once rare has now become extremely abundant. For observations on the structure and metamorphoses of *Cartodere* see Dingler (*Zeits. f. angewandte Entom.* 14, 1928).

FAM. MYCETOPHAGIDÆ.—TARSI SLENDER, 4-JOINTED, THOSE OF ANTERIOR LEGS 3-JOINTED IN MALE: COXÆ OVAL. ABDOMEN WITH FIVE, FREE, EQUAL STERNA. The members of this small family chiefly live in rotting wood or under bark, associated with fungi: about a dozen species occur in Britain. Their larvæ (vide Perris) are elongate and cylindrical with 4-jointed antennæ and the 9th abdominal segment terminates in a pair of smooth chitinous processes.

FAM. COLYDIIDÆ.—TARSI USUALLY 4-JOINTED WITH THE 3RD JOINT NORMAL: FORE AND MIDDLE COXÆ SMALL AND GLOBOSE, HIND COXÆ TRANSVERSE. ABDOMEN WITH FIVE STERNA, THE FIRST THREE OR FOUR MORE OR LESS CONNATE. A family of usually elongate and more or less cylindrical beetles found beneath bark and in wood or fungi: a few species occur below ground or among vegetable refuse. Sharp remarks that the species exhibit great diversity of sculpture and clothing and are mainly restricted to primæval forests. They disappear entirely when these are destroyed: New Zealand has produced 170 species as compared with only 19 found in Britain. The larvæ are very like those of the preceding family except that there are usually spines or tubercles associated with the terminal chitinous processes. Very little is known concerning their habits but they are probably mostly predaceous: the larvæ of several species of *Bothrideres* have been noted to be ectoparasites of other coleopterous larvæ in America. The neotropical **ADIMERIDÆ** consist of a single genus characterized by the unique structure of the tarsi.

FAM. ENDOMYCHIDÆ.—TARSI APPARENTLY 3-JOINTED, THE 1ST TWO JOINTS BROAD, THE 3RD MINUTE AND THE TERMINAL JOINT ELONGATE: FORE AND MIDDLE COXÆ GLOBOSE. FIVE OR SIX FREE ABDOMINAL STERNA. A family of about 600 species chiefly met with among fungi on timber in tropical forests. Many have brilliant colours and are variable in form and size. Among the few British species the black and red *Endomychus coccineus* and the minute *Mycetæa hirta* are the best known. The latter occurs in dung, vegetable refuse and often in wine cellars. The larvæ are broader and more ovate than those of allied families and have the lateral margins of the abdominal tergites expanded so as to conceal the pleura: the 9th segment has no chitinous projections. Those of two species described by Bates are conspicuously marked with black and yellow.

FAM. COCCINELLIDÆ (Lady-birds).—USUALLY ROUNDED AND CONVEX INSECTS WITH THE HEAD MUCH CONCEALED BY THE THORAX: ANTENNÆ FEEBLY CLAVATE. TARSI APPARENTLY 3-JOINTED OWING TO THE MINUTE CONCEALED THIRD JOINT. This very important family comprises well over 2,000 species, for the most part brightly coloured and spotted. The family is very closely related to the Endomychidæ but differs in the irregularly triangular mesepimera, and the small antennæ: in the Endomychidæ the mesepimera are quadrilateral, and the antennæ larger. The greater number of the species are carnivorous and predaceous, feeding during the larval and adult stages upon aphids, coccids and occasionally on other soft-bodied insects. They are, therefore, of very great importance in reducing the numbers of injurious species. A comparatively small group are phytophagous but they rarely cause serious damage. Structurally, the carnivorous forms (Coccinellinæ) are characterized by the mandibles having simple or bifid apices and each jaw being armed with a basal tooth. The herbivorous species (Epilacninæ) lack the basal tooth and the apex of the mandible is multidentate. The Lithophilinæ form a third subfamily: very little is known about their habits but the mandibles are of the carnivorous type. They are distinguished by the tarsi being evidently 4-jointed.

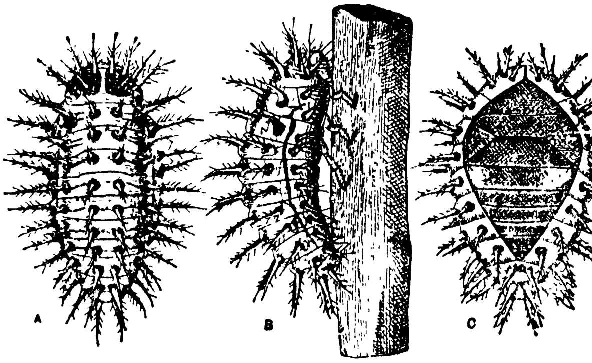

FIG. 494.—LARVA OF *CHILOCORUS*. A, DORSAL; B, LATERAL; C, PUPA.

After Silvestri.

When disturbed many members of the family discharge a bitter, amber-coloured fluid. It is usually emitted through pores situated around the tibio-femoral articulations, but in *Epilachna* the pores have a much wider distribution. According to McIndoo (*Ann. Ent. Soc. Am.*, 9) the exuded liquid is a secretory product of hypodermal gland cells: other writers have regarded it as the blood of the insect. Porta (*Anat Anz.*, 1903) found that the secretion had a poisonous effect upon vertebrates but had no influence upon insects. It is regarded as defensive in function, but it must be pointed out that Coccinellids are known to be eaten by several species of birds.

Several members of the family, notably *Coccinella variabilis* and *Adalia bipunctata* (Fig. 495), are remarkable for their wide range of colour variation, the latter species having over two dozen named varieties. Another peculiarity is the markedly gregarious habits of certain species both during hibernation and when in the open: at times these insects have been found in " masses " but the meaning of the phenomenon is obscure. One of the best known members of the family is *Novius cardinalis* which has been imported from Australia into California for purposes of controlling *Icerya purchasi*—a serious enemy of Citrus cultivation in the latter country. The beetle proved so effective a controlling agent that it has since been imported into all countries where the coccid has become injurious.

Coccinellid larvæ (vide Böving, 1917) are soft bodied and variously coloured: they are often of a leaden or other dark hue spotted with yellow or white. There are three ocelli on either side, the mandibles are sickle-shaped with molar bases (except in the Epilachninæ) and the legs are long and slender. The terga are usually provided with segmental tubercles and spines and the abdomen tapers distally, but never bears the chitinous processes so characteristic of other families. In some genera (*Hyperaspis*, *Scymnus* and *Platynaspis*) the spines are wanting and the whole body is covered with a white flocculent secretion. In *Chilocorus* (Fig. 494) the body is protected by long integumental processes.

The usual number of instars appears to be four, and the complete development of *Adalia bipunctata* in England was found to occupy about 34 days in captivity (Hawkes, *Proc. Zool. Soc.* 1920), an average of 20 days being spent as a larva. In California, Clausen (*Journ. Econ. Ent.* 1915) found the average developmental period was 26 days. The eggs of Coccinellids are yellow, and disposed in batches, with their long axes perpendicular to the surface of the leaves upon which they are laid. Palmer found that the number laid by *Coccinella 9-notata* varied from 435 to 1,047: in *A. bipunctata* Hawkes states that the average number lies between 140 and 148 with 418 as the maximum. The number of aphids daily consumed by the larva of this species is stated by Clausen to be 14 while in *Coccinella californica* it is about 20. During the entire larval period he found that the number consumed varied between 216 and 475 for different species: the adults are usually even more voracious. *Hyperaspis binotata* is a coccid feeder and according to Simanton (*Journ. Agric. Res.* 6) it will destroy 90 adults and 3,000 larvæ during its period of larval existence. When about to pupate, Coccinellid larvæ usually suspend themselves by the caudal extremity which is attached by means of a secretion to plants, palings and other objects. The pupæ are usually conspicuously coloured and are either surrounded by the larval exuviæ, or the latter are pushed back to the anal extremity.

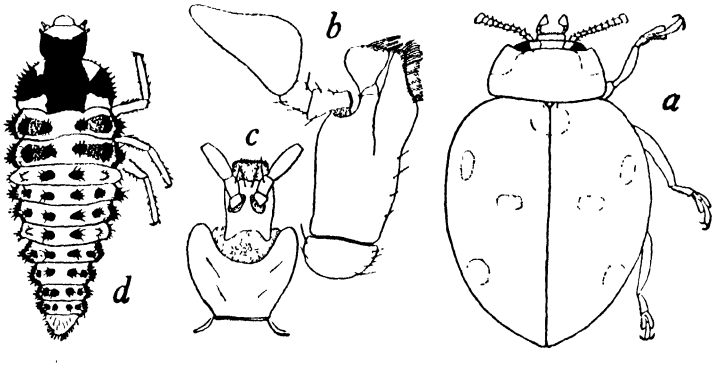

FIG. 495.—COCCINELLIDÆ.

a, Coccinella septempunctata; *b*, maxilla; *c*, labium; *d*, a coccinellid larva. All magnified.

The larvæ of the Epilachninæ (vide Grandi, *Boll. Lab. Zool. Portici*, 7) are invested with long branched processes of the body-wall. Members of this subfamily are often destructive to the foliage of potatoes, Cucurbitaceæ, etc., especially in N. America. The only British member of the group is *Subcoccinella 24-punctata* whose larva gnaws the parenchyma of clover and other plants.

For further information on the biology of the family, vide Gage (*Illinois Biol. Monog.* 6, 1920), Palmer (*Ann. Ent. Soc. Am.* 7) and papers by the latter writer on colour-inheritance in *Adalia* (*Ibid.* 4 and 10). Donisthorpe (*Ent. Record*, 1919, 1920) has followed the complete life-history of *Coccinella distincta*—a species found in association with ants.

Carpet beetles.

FAM. DERMESTIDÆ.—ANTENNÆ USUALLY SHORT WITH THE CLUB OFTEN RELATIVELY LARGE AND WITH THE UNDERSIDE OF THE THORAX BEARING A HOLLOW FOR ITS RECEPTION. TARSI 5-JOINTED: FORE COXA RATHER LONG, OBLIQUE: HIND COXA FORMED TO RECEIVE THE FEMUR IN REPOSE. A family of small or moderate sized beetles usually invested with fine hair or with scales. They mostly inhabit furs, hides, wool and other integumentary substances as well as bacon, cheese, etc., and are exceedingly destructive as larvæ. Some from their habits, have become almost cosmopolitan and 16 species occur in Britain. Out in the field many act as scavengers in removing offensive animal matter. The adults of *Anthrenus* have been found in natural history specimens and also on flowers: its larvæ are extremely destructive, and are the enemy of the collector. *Tiresias* occurs under loose bark among cobwebs, probably feeding upon the insect remains present. *Dermestes* includes many species, some of which occur in dead animals and others are more frequently met with in dwellings, museums, etc., where they attack hides, furs, bacon, etc. The larvæ of this family (vide Kreyenbergh, 1928) differ completely from those of other Coleoptera. Their upper surface is covered with a complex clothing of hairs of various lengths. The hairs are often aggregated into terminal or lateral tufts which, in some cases at least, can be raised at will or even rapidly vibrated: the function of this investment appears to be unknown. When a larva is about to pupate the integument splits down the back and remains as a pupal covering.

FAM. BYRRHIDÆ (Pill Beetles).—VERY CONVEX, OVAL OR ROUND INSECTS WITH RETRACTED HEAD : FORE COXÆ TRANSVERSE, NOT EXSERTED, HIND COXÆ SHIELDING THE RETRACTED FEMORA. ALL THE APPENDAGES CAPABLE OF BEING CLOSELY ADPRESSED TO THE BODY. The members of this family mostly occur on the ground beneath stones, at roots of grasses or in moss. Their most striking feature is the power these beetles have of withdrawing their appendages in close contact with the body and remaining motionless : in this attitude they are hard to detect and often closely resemble their surroundings. According to Sharp it is not clear whether this family can be separated from the Parnidæ or the Dascillidæ, and its sub-families have little connection beyond the common faculty of closely retracting their appendages to the body. The Chelonariinæ are mostly tropical and occur on the leaves of plants : they are very different from other of the Byrrhidæ in that the antennæ are filiform instead of being clubbed, and are inserted on the front. The best known British species of the family is *Byrrhus pilula*, which is often found on paths in spring. Its life-history is in need of investigation and, according to Chapuis and Candèze, the larva is cylindrical and fleshy and may be recognized by the large size and breadth of the prothorax and the last two abdominal segments. The head is short and broad, the antennæ very short and there is a pair of ocelli on either side. The pronotum is markedly chitinized and sculptured, and the last abdominal segment carries a pair of retractile locomotory processes. The larva occurs beneath turf or moss and is about 18 mm. long. The **NOSODENDRIDÆ** are often included in this family but are separable on account of the prominent head and the large mentum. The single genus *Nosodendron* is very widely distributed and its curious larva is figured by Ganglbauer. The **CYATHOCERIDÆ** consist of a single species found in South America and the **GEORYSSIDÆ** are probably almost world-wide. *Georyssus* is represented in Britain by *G. pygmæus* which frequents very wet situations : the tarsi are 4-jointed and the anterior coxæ laminate.

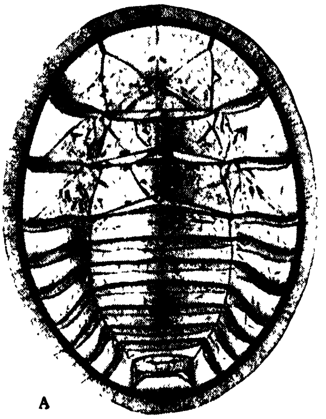

FIG. 496.—A PSEPHENID LARVA, HIMALAYA. A, DORSAL; B, VENTRAL. × 15.

FAM. DRYOPIDÆ (Parnidæ).—HEAD RETRACTILE, THE MOUTH PROTECTED BY THE PROSTERNUM. THE LATTER DISTINCT IN FRONT OF THE COXÆ, BEHIND FORMING A PROCESS RECEIVED INTO A DEFINITE CAVITY OF THE MESOSTERNUM. TARSI 5-JOINTED, TERMINAL JOINT LONG, CLAWS LARGE. The members of this family are found, for the most part, near running water or clinging by means of their strong claws to water plants and other submerged objects. They have no powers of swimming and the three sub-families into which they are grouped show very diverse affinities, being sometimes regarded as separate families. The Psepheninæ are interesting on account of their remarkable larvæ (Fig. 496). The latter occur in swift rivers and in waterfalls, *Psephenus* being especially abundant in the rapids of Niagara, while larvæ of this and other genera are also plentiful in the Himalayan rivers. They are flattened, rounded or ovoid and almost scale-like in form : the margins of the body are greatly expanded and consequently the appendages are not visible from above. They cling with great tenacity to stones, etc., and the whole body appears to act in a sucker-like fashion rendering these larvæ difficult to remove. Respiration takes place either by means of abdominal gills, or by the aid of a retractile tuft of anal filaments which is only visible in the undisturbed living larva. The pupæ are submerged and soldered down to the stones upon which the larval life was passed : they closely resemble the larvæ when viewed from above, but are armed with curious tufts of long setæ. The Dryopinæ like the Psepheninæ are densely pubescent beetles and are thus enabled to carry a film of air with them for respiration under water : the antennæ are very short and of more or less irregular form. The larva of *Dryops* Oliv. (*Parnus* F.) is stated to live in damp earth beneath stones and to resemble those of the Elateridæ: several species of the genus occur in Britain. The Elminæ differ from the Dryopinæ in having the anterior coxæ globular: the body is bare or feebly pubescent and the antennæ simple. Three genera are British: the larva of *Macronychus* is figured by Perris and that of *Elmis* by Chapuis and Candèze.

FAM. HYDROPHILIDÆ.—AQUATIC OR SUBAQUATIC WITH SHORT 6 TO 9-JOINTED ANTENNÆ TERMINATING IN A PUBESCENT CLUB. MAXILLARY PALPI ELONGATE, OFTEN MUCH LONGER THAN ANTENNÆ. TARSI 5-JOINTED, FIRST JOINT OFTEN MINUTE. A large family comprising about 1,000 species which are especially numerous in the tropics. The adults live upon decomposing vegetable matter and, in many cases, the larvæ have a similar habit but those of *Hydrophilus* (*Hydrous* Lch.) and its allies are predaceous. A large number of the species have elongate maxillary palpi (Fig. 459) and, on this account, the family has often been termed the Palpicornia: this character, however, is not always very evident. The long palpi perform the functions of antennæ, the latter organs being used in respiration by the submerged insect. Although a large number of the Hydrophilidæ are truly aquatic, the family name is inappropriate as a considerable number are land insects. The latter are met with in damp or marshy places or among vegetable refuse, while *Cercyon* and *Sphæridium* are common in dung. One of the best known members of the family is *Hydrophilus piceus* which is almost the largest British Coleopteron. It is less perfectly adapted for swimming than *Dytiscus* and does not require the agility that characterizes predaceous insects. Much has been written on this species, especially with reference to its peculiar mode of respiration. A dorsal air-reservoir is present beneath the elytra and there are ventral hairy tracts which also serve to retain an air-film. On either side of the thorax and abdomen there is a longitudinal tract of delicate pubescence bounded above by the overhanging edges of the prothorax and elytra. The spiracles open into these linear tracts, and the latter also communicate with the dorsal air-reservoir. When the insect rises to renew its air supply the body is slightly inclined to one side so as to bring the angle between the head and prothorax, on one side of the body, to the surface. The hairy antennæ club plays an important part in breaking the surface film, and facilitating the entry of air into the cleft already mentioned, and its passage into the lateral tracts. The complete details of the respiratory process are too lengthy for discussion here and the student is referred to the works of Miall (1912), Portier (1911), Brocher and others.

The eggs of *Hydrophilus, Hydrocharis* (*Hydrous* Brullé) *Hydrobius* and other genera are enclosed in cocoons of a remarkable construction (vide Portier): the latter are usually attached to grass or floating objects, but *Helochares* and *Spercheus* fasten them to their own bodies. The larvæ of the family do not admit of any general description on account of their great diversity of form and structure: those of a number of forms have been studied by Schiödte and later by d'Orchymont (*Ann. Biol. Lacus.* 6). Several of the aquatic genera, including *Hydrophilus*, are metapneustic and the spiracles are placed on the last body segment in a kind of atrium. *Hydrocharis* and *Berosus* have long fringed gill-like structures on the first seven abdominal segments: in *Helophorus aquaticus* the larva is strongly chitinized, the thoracic terga are entire, and each of the first eight abdominal segments is protected by four transverse plates. The larvæ of *Cercyon* and *Sphæridium* are degenerate and grub-like with the legs atrophied or vestigial. In the majority of the larvæ of this family cerci are present and sometimes elongate.

FAM. HETEROCERIDÆ.—LABRUM AND MANDIBLES PROMINENT AND PROJECTING: ANTENNÆ SHORT, THE LAST SEVEN JOINTS FORMING A BROAD SERRATE CLUB. LEGS SPINOSE, ADAPTED FOR DIGGING: TARSI 4-JOINTED. These small beetles are densely pubescent and live in galleries which they excavate in the mud bordering pools and streams. Their larvæ inhabit the same situations and may be recognized by the prominent mandibles, the very broad thoracic segments and the much narrower abdomen: the whole body is strongly setose. The family is very widely distributed and about 100 species are known, several being indigenous to the British Isles.

The remaining families of the Diversicornia constitute the old series SERRICORNIA. With comparatively few exceptions the tarsi are 5-jointed: the antennæ, on the other hand, are extremely variable. They may be filiform, serrate, clavate (rarely). clavate-serrate or even plumose.

FAM. DASCILLIDÆ.—ANTENNÆ SERRATE, RARELY PECTINATE OR FLABELLATE, ANTERIOR AND POSTERIOR COXÆ TRANSVERSE, THE FORMER WITH A LARGE TROCHANTIN, THE LATTER FORMING A PLATE FOR THE RECEPTION OF THE FEMUR. These rather small beetles are represented in Britain by *Dascillus*, which principally occurs in flowers:

its larva has been found at the roots of grasses in pasture land and is figured by Gahan (*Trans. Ent. Soc.* 1908).

FAM. HELODIDÆ.—DIFFERING FROM DASCILLIDÆ IN THE FILIFORM ANTENNÆ AND THE ABSENCE OF THE TROCHANTIN TO THE ANTERIOR COXÆ. These small insects have a very thin integument and loosely articulated legs. They occur among herbage, mostly in damp situations, and their larvæ are aquatic. About 16 species are British and a well illustrated account of the structure and biology of *Scirtes hemisphericus* is given by Lombardi in *Bull. Lab. Entom. Inst. Agrario, Bologna*, 1928.

FAM. RHIPICERIDÆ.—RATHER LARGE INSECTS WITH CONSPICUOUSLY FLABELLATE ANTENNÆ, PARTICULARLY IN THE MALES. MANDIBLES ROBUST AND STRONGLY CURVED. EMPODIA LARGE AND HAIRY. A small family confined to the warmer regions of the world and found on trees or low plants. The larva of *Callirhipis* somewhat resembles that of *Tenebrio* and is described in great detail by Schiödte.

FAM. CANTHARIDÆ (Telephoridæ : Malacodermidæ).—VERY SOFT BODIED USUALLY ELONGATE INSECTS WITH LONG SLENDER LEGS. ANTENNÆ OF VARIOUS FORMS. ABDOMEN WITH SEVEN OR EIGHT VISIBLE STERNA, THE BASAL REGION NOT COADAPTED IN FORM WITH THE COXÆ. ANTERIOR AND MIDDLE COXÆ CONICO-CYLINDRICAL, THE FORMER WITH DISTINCT TROCHANTINS : POSTERIOR COXÆ TRANSVERSE. — This very large family includes some of the most familiar of all Coleoptera and numbers about 4,000 species.

The Lycinæ are diurnal and are found on leaves and flowers or under bark : the few British members of this sub-family are rare and local. The group is chiefly tropical and its members are stated to be carnivorous. Mjoberg (vide *Psyche*, 1926) describes and figures the curious trilobite-like female of *Duliticola* and it is probable that other examples of this type have often been regarded as larvæ.

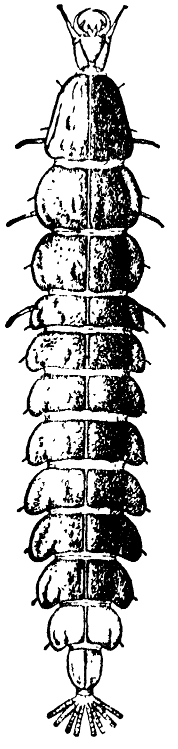

FIG. 497.—*Luciola lusitanica*, Larva × 8. France. *After* Bugnion.

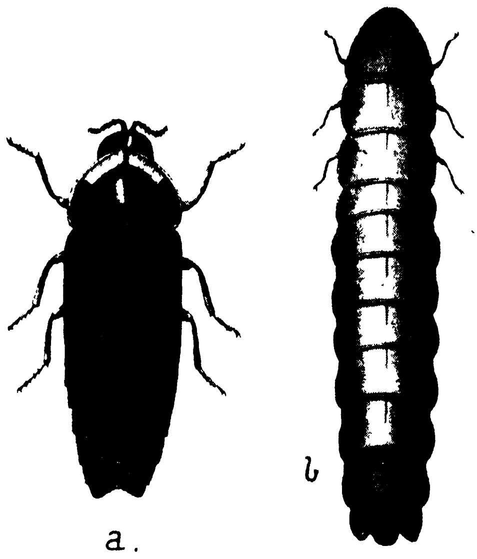

FIG. 498.—*Lamprophorus tardus*, India. *a*, Male × 2 : *b*, Female, Nat. Size.

The Lampyrinæ include the "glow-worms" and "fireflies" : they number more than 2,000 species which differ from the Lycinæ in having the middle coxæ contiguous, whereas, in the latter group, they are spaced apart. They are nocturnal insects, and most of the members are provided with photogenic organs which emit a more or less bright light usually, although not invariably, strongest in the female. These organs are borne on certain of the hind segments of the abdomen,—often the 6th and 7th in the male, and the latter segment in the female : in *Phausis* and *Phengodes* they show a wider distribution. The eggs, larvæ and pupæ are also luminous to a variable degree. There is an extensive literature on the structure and physiology of the photogenic organs (vide p.105) : as a rule the light is pale yellowish green, but Haase mentions certain S. American species whose larvæ emit two series of lights —red and green. The function of this luminescence is difficult to conceive with reference to the immature stages but, in the adults, it serves in most cases to bring the sexes together. In many forms the male is winged with greatly developed eyes, and the female devoid of both elytra and wings (vide Fig. 498), being larviform with the eyes small. This dimorphism is well exhibited in the common European "glow-worm" *Lampyris noctiluca*. The biology of this insect has been studied by Newport (1857), Fabre, and others, and its larva by Vogel (1915). The adult insect takes little or no food, but the larvæ are carnivorous, feeding upon snails and slugs, which they seize with their sharp sickle-like mandibles. The latter are each traversed by a fine canal through which a dark-coloured secretion is injected into the tissues of the prey. As there are no salivary glands, the secretion is apparently produced by a pair of acinose glands near the anterior end of the mid-gut. According to Bugnion (*Bull. Soc. Vaud.* 1915) they probably open at the base of the mandibles. The secretion has the property of breaking down the tissues of the mollusc, and digestion is largely external, the larva imbibing its prepared meal by means of the pumping action of its pharynx. Unlike the *Dytiscus* larva, the food appears to be taken in through the mouth which is guarded by a mass of hairs precluding the entry of anything excepting small particles. The larvæ of *Photinus* and *Photuris* have been studied by Williams (1917) and their photogenic organs are situated on the 8th abdominal segment. They persist in the pupa but are replaced in the imago by structures located on the 6th and 7th segments. In the Mediterranean " fire-flies " (*Luciola*) both sexes are winged. They are gregarious, but the females are more imperfect than the males and are rarely seen. The function of the light is obscure, and it is most brilliant in the males.

The Cantharinæ have no photogenic organs and the sexes are very alike. Some of the best known members are species of *Cantharis* (*Telephorus*) and *Rhagonycha*, often called " soldier beetles," which are predaceous and frequent flowers and herbage. Their somewhat flattened larvæ are found in the soil or among moss, etc. They are primarily carnivorous, and have a velvety appearance due to a covering of fine hairs (vide Payne, 1916). The head is flat, the antennæ short, and there is a single ocellus behind each: the anal segment has a ventral pseudopod but there are no cerci.

The Drilinæ exhibit a sexual dimorphism even more striking than that seen in *Lampyris*, the apterous females being enormously large in proportion to the males. The larva of *Drilus flavescens* preys upon snails (vide Crawshay, *Trans. Ent. Soc.* 1903).

FAM. MELYDRIDÆ (Malachiidæ).—CLOSELY ALLIED TO THE CANTHARIDÆ, BUT THE ABDOMEN WITH ONLY SIX STERNA, AND THE BASE MORE OR LESS CO-ADAPTED WITH THE COXÆ. This family includes about 1,000 species which mostly resemble the Cantharinæ in their general facies: it is represented in Britain by nine genera and about a score of species. *Malachius* and its allies frequent flowers, and are characterized by the presence of the lateral protrusible vesicles at the sides of the thorax and abdomen. Their larvæ are stated by Perris to resemble those of *Cantharis*.

FAM. CLERIDÆ.—ANTENNÆ VARIOUS, SOMETIMES CLUBBED; LABIAL PALPI DILATED AND SECURIFORM. TARSI 5-JOINTED, BUT SOMETIMES APPARENTLY 4-JOINTED: APICES OF JOINTS TWO TO FOUR USUALLY PROLONGED AS MEMBRANOUS FLAPS. ANTERIOR COXÆ PROMINENT, CONTIGUOUS. ABDOMEN WITH FIVE OR SIX FREE STERNA. An extensive family, mainly tropical, many of whose members are of graceful form and beautiful coloration. They are mostly found on plants or tree-trunks, but a few (*Necrobia*, *Corynetes*) occur in carcasses and skins. In the larval stage they are mostly predaceous and beneficial, since they feed upon wood- and bark-boring Coleoptera. *Necrobia* probably feeds upon saprophagous matter and also upon dipterous larvæ of the same habit; the nearly cosmopolitan *N. rufipes* is destructive to stored hams. *Corynetes* sometimes preys upon *Anobium*, and *Trichodes* is known to infest the nests of *Apis*, *Chalicodoma* and other bees. The general appearance of Clerid larvæ can be gathered from a valuable paper by Boving and Champlain (1920), and also from an article by Boving (*Ent. Tidskr.*, 1913). They are frequently bright red, brown, pink or otherwise vividly coloured, and are more or less elongate and cylindrical, or slightly flattened. The pronotum is strongly chitinized but the remaining segments are usually fleshy except the 9th, which carries a hard shield bearing two corneous processes, and the abdomen often has ambulatory swellings.

FAM. LYMEXYLONIDÆ.—VERY ELONGATE INSECTS WITH SOFT INTEGUMENT AND SHORT, BROAD, SERRATE ANTENNÆ. MAXILLARY PALPI IN MALE LARGE AND FLABELLATE. FORE AND MIDDLE COXÆ EXSERTED, LONGITUDINAL IN POSITION: TARSI FILIFORM. ABDOMEN WITH 5 TO 8 STERNA. This small family is nearly world-wide and includes some very remarkable species capable of boring into hard wood and doing at times considerable damage by drilling cylindrical holes. The curious larvæ of *Lymexylon* and *Hylecœtus* are figured by Westwood (Classif. I, p. 269) and that of *Melittomma* by Gahan (*Trans. Ent. Soc.* 1908). The remarkable oriental genus *Atractocerus* has rudimentary elytra, but ample wings, and its long flexible abdomen gives its species the appearance of Staphylinids. The N. American **MICROMALTHIDÆ** consist of a single species of *Micromalthus* which was formerly placed in the Lymexylonidæ, but differs in the maxillary palpi of the male being simple. The biology of this insect, according to Barber (1913), is one of the most remarkable in the whole of the Insecta. It combines in its life-cycle seven or eight forms of larvæ and exhibits both oviparous and viviparous pædogenesis.

FAM. ANOBIIDÆ (Ptinidæ).—FIRST TARSAL JOINT NOT REDUCED IN SIZE, OFTEN LONGER THAN SECOND. PROSTERNUM VERY SHORT: FORE AND MIDDLE COXÆ SMALL, NOT TRANSVERSELY EXTENDED, THE FORMER SLIGHTLY PROMINENT: HIND COXÆ TRANSVERSE. ABDOMEN WITH FIVE VISIBLE STERNA OF EQUAL LENGTH. Included in this family are the Ptinides and Anobiides which are regarded by many authors as separate families. According to Sharp it is probable that scarcely more than one-fiftieth part of the existing species have been described, their concealed habits rendering them difficult to find. Many are very destructive to wood and to various kinds of stored products. They are either globular or cylindrical in form, often very different in the sexes. In the Ptinides the antennæ are long and filiform, while in the Anobiides they are either serrate, pectinate or loosely clubbed. Their larvæ (vide Munro, 1915) resemble those of the Lamellicornia in their crescentic form; they are likewise fleshy and the terminal abdominal segments are generally larger than those preceding. The antennæ are very short and there are no anal processes or cerci. *Ptinus fur* is destructive to books, furs, woollen goods, drugs, herbaria, etc. *Anobium punctatum* De G. (*striatum* Oliv.) and *Xestobium rufovillosum* De G. (*tesselatum* Oliv.) are very destructive to furniture, rafters and flooring, their larvæ boring into the solid wood (Fig. 499): the small round exit holes made by the adult beetles are very familiar objects. The name of "death watch" is often applied to both these species but belongs more properly to the latter insect. The tapping noise is a sexual call and is heard most often in April to May when pairing takes place. The beetle jerks its body forward several times in rapid succession, each time striking the lower part of the front of the head against the surface upon which it is standing (Gahan). *Lasioderma serricorne* and *Sitodrepa paniceum* are cosmopolitan: they injure a great variety of stored materials, etc. The former species attacks cigarettes, cigars, drugs, ginger, etc., and the latter is destructive to biscuits, flour, bread, many drugs including opium and aconite, together with a wide range of other substances. The Australian **ECTREPHIDÆ** are myrmecophilous and possibly belong here: Wasmann, on the other hand, considers that they are allied to the Scydmænidæ.

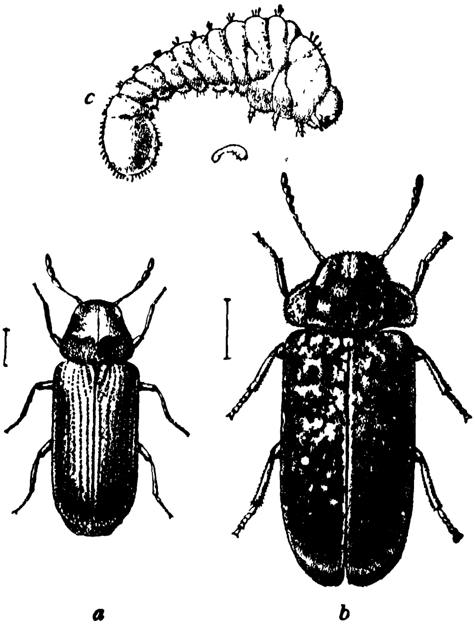

FIG. 499.—*a*, *Anobium punctatum*; *c*, Its Larva; *b*, *Xestobium rufovillosum*.

After Gahan (reproduced by permission of the Trustees of the British Museum).

FAM. BOSTRICHIDÆ (Apatidæ).—FORM CYLINDRICAL, HEAD USUALLY DEFLEXED AND COVERED BY THE HOOD-SHAPED PRONOTUM: ANTENNÆ WITH A 3-JOINTED CLUB. FIRST TARSAL JOINT MINUTE. FORE COXÆ PROMINENT, CONTIGUOUS BUT LITTLE EXTENDED TRANSVERSELY. ABDOMEN WITH FIVE VISIBLE STERNA OF EQUAL LENGTH. The members of this family make cylindrical burrows in felled timber or dried wood, and occasionally attack unhealthy standing trees. They exhibit a great variety of sculpture while the body is often truncated posteriorly and armed with small projections. Species of *Sinoxylon* and *Dinoderus* are very destructive to felled trees and bamboo in India. Their larvæ resemble those of the Ptinidæ and are similarly curved posteriorly, but the head is greatly reduced and the thorax more enlarged: the larva of *Apate capucina* is figured by Perris, Ratzeburg and others. The family is world-wide but only represented in Britain by a few rare species.

FAM. LYCTIDÆ (Powder Post Beetles).—DIFFERING FROM THE BOSTRICHIDÆ IN THE 2-JOINTED ANTENNAL CLUB AND THE ELONGATE 1ST ABDOMINAL STERNUM. This family is closely allied to the one preceding and is often merged as one of its groups. The larvæ also are very similar and Lameere was of opinion that this similarity overweighed any adult differences. They are small elongate insects, found both in freshly cut and old timber, palings and furniture · only the wood of broad-leaved trees appears to be attacked. *Lyctus* larvæ are often mistaken for those of the Ptinidæ but may be easily distinguished by the legs being 3-jointed, whereas they are 5-jointed in the latter family (vide Munro, 1915). The Lyctidæ are few in species and several occur in the British Isles (Fig. 500).

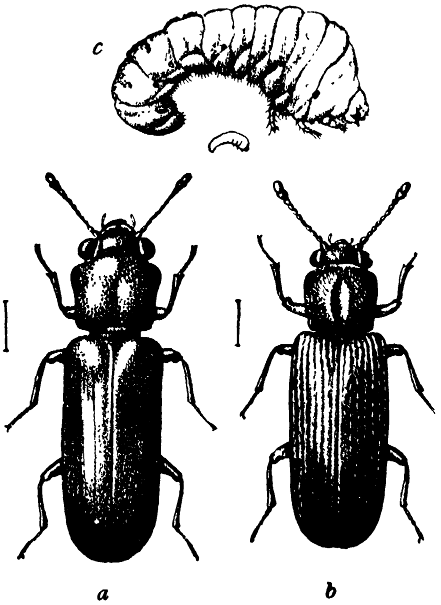

Fig. 500.—*a*, *Lyctus brunneus*; *c*, Its Larva; *b*, *Lyctus linearis*.

After Gahan (reproduced by permission of the Trustees of the British Museum).

FAM. CIOIDÆ (**Cissidæ**).—MINUTE CYLINDRICAL INSECTS WITH SHORT CLAVATE ANTENNÆ AND 4-JOINTED TARSI. FORE AND MIDDLE COXÆ SMALL, OVAL, NOT PROMINENT. ABDOMEN WITH 5 MOBILE STERNA. A widely distributed family comprising probably over 300 described species found in old wood or fungi and usually of gregarious habits. Their affinities are by no means settled and Sharp states that the position of these insects seems to be near the Colydiidæ and Cryptophagidæ. *Cis* is nearly world-wide in distribution and is represented by more than a dozen species in Britain: its elongate cylindrical larva is described in a monograph by Mellié (*Ann. Soc. Ent. Fr.* 1848). The **SPHINDIDÆ** are usually placed near this family and consist of minute insects living under bark or in fungi. *Sphindus* and *Aspidiphorus* occur in Britain and their larvæ are described by Perris.

FAM. BUPRESTIDÆ.—USUALLY CONSPICUOUS METALLIC INSECTS WITH SHORT SERRATE ANTENNÆ. PROTHORAX CLOSELY ADAPTED TO THE AFTER BODY WITH A PROCESS FITTING INTO THE CAVITY OF THE MESOSTERNUM BUT NOT ALLOWING OF SALTATORY MOVEMENTS. FIVE VISIBLE STERNA, THE FIRST TWO CONNATE, REMAINDER MOBILE. An essentially tropical family comprising over 5,000 species; relatively few are European and only four genera with ten species occur in Britain. They are among the most brilliantly coloured of all insects and some species, owing to the splendour of their metallic lustre, are used in embroidery and in jewellery (Fig. 501). They are typically inhabitants of hot moist forests and are exceedingly active on the wing, often taking flight at the least alarm. The larvæ (vide Xambeu, *Rev. d'Ent.* 1892–93) are distinct from those of other Coleoptera, and characterized by the great expansion of the prothorax and the slender hind-body which imparts to them a clubbed appearance (Fig. 502). The head is small and almost entirely withdrawn into the thorax, the antennæ extremely short, and there are no ocelli. The legs are vestigial or absent, the abdominal segments are nine in number and there are no cerci or anal processes. There are nine pairs of spiracles, the first pair being situated between the pro- and meso-thorax or on the latter segment. The larvæ mostly gnaw rather broad flattened galleries in or beneath the bark of trees or in roots: some are found in the stems of herbaceous plants and one or two mine leaves. Some of the genera of this family are exceedingly large: *Agrilus* comprises nearly 700 species while *Sphenoptera* and *Chrysobothris* each include about 300. For further information on the family reference should be made to the work of Kerremans (1906–14).

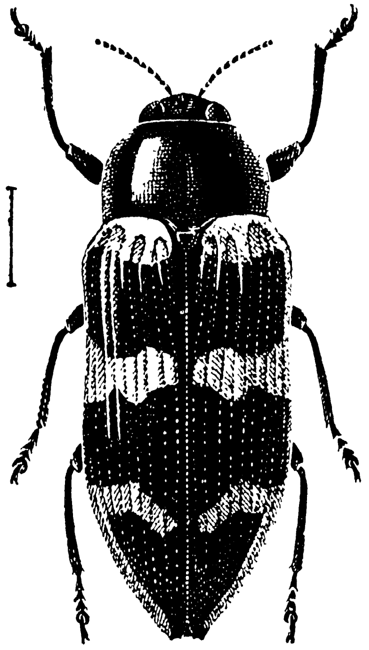

Fig. 501.—*Stigmadera interstitialis.* Australia.

After Carter (actual size).

FAM. ELATERIDÆ (Click Beetles).—ANTENNÆ SERRATE, PECTINATE OR FILIFORM. PROTHORAX WITH HIND ANGLES GENERALLY PRODUCED: WITH A PROSTERNAL PROCESS THAT IS RECEIVED IN A MESOSTERNAL CAVITY. ANTERIOR COXAL CAVITIES FORMED ENTIRELY BY THE PROSTERNUM: HIND COXÆ WITH A PLATE UNDERLYING THE FEMUR. LEGS RATHER SHORT, OFTEN RETRACTILE. FIVE ABDOMINAL STERNA, THE LAST ALONE BEING MOBILE. A large and very important family of wide distribution. Its subdivision is not in a very satisfactory condition and the subfamilies here recognized have been regarded by Lacordaire and others as separate families. A few of the Eucneminæ and most of the Elaterinæ possess the power of leaping when lying on their back. The mechanism of this act is not entirely clear, but the existence of the saltatory power is connected with the mobility of the articulation between the pro- and meso-thorax. As a preliminary, the apex of the prosternal process catches against the edge of the mesosternal cavity. When, however, the process slips over the catch it is driven with considerable force into the mesosternal cavity accompanied by a clicking sound. The force imparted by this jerking movement causes the bases of the elytra to strike the surface upon which the insect is resting and this, together with the elasticity of the elytra, appears to be the chief factor in bringing about the leap. (Fig. 508*b*).

The sub-family Eucneminæ is distinguished from the genuine Elaterinæ by the antennæ being somewhat distant from the eyes. They are chiefly noteworthy on account of their larvæ which are apodous. The latter live in soft wood, and the head is armed with hard teeth for boring purposes, the maxillæ and labium being vestigial. The statement that they are carnivorous is probably erroneous, and their food is more likely derived from decaying wood. ***Melasis*** *buprestoides* is the only species at all plentiful in Britain, and its larva is figured by Schiödte. It much resembles that of a Buprestid but is separable on account of the vestigial mouthparts.

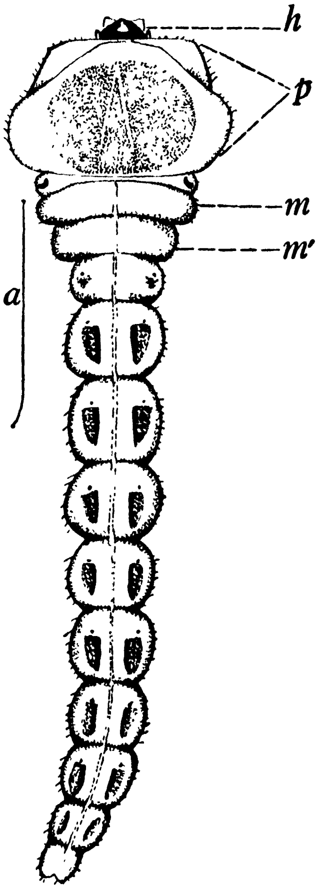

FIG. 502.—*CHRYSOBOTHRIS*, LARVA.

a, actual length, *h*, head; *p*, prothorax; *m*, mesothorax; *m'*, metathorax

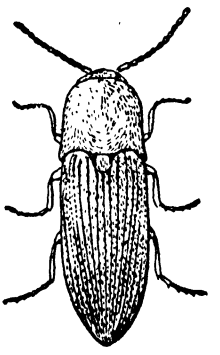

FIG. 503.—*AGRIOTES OBSCURUS*, EUROPE × 4.

(Reproduced by permission of the Ministry of Agriculture).

The Elaterinæ have the antennæ inserted near the eyes. They are mostly sombre coloured elongate insects, but a few are red or have metallic colours. The most remarkable species are the "fire-flies" (*Pyrophorus*) which are mainly neotropical. *P. noctilucus* emits an exceptionally bright light from a rounded yellow area in either side of the thorax and, when on the wing, an additional source of light is revealed at the base of the ventral surface of the abdomen. The eggs and larvæ are also luminous. In the young larva the photogenic organ is situated at the junction of the head and thorax: in older larvæ there are numerous small lateral organs in addition. The photogenic organs are very similar in structure to those of the Lampyrinæ and are dealt with on p. 104 The larvæ of the Elaterinæ are elongate and cylindrical and very tough-skinned (Fig. 505). The head is corneous and flattened, the antennæ very short and 3-jointed, eyes are present, the labrum is not defined, and the trunk segments are very alike. The whole body is usually reddish-brown or yellow, owing to the strong chitinization of all the segments, and the legs are short. The prothorax is the largest, and the 9th segment is specially differentiated and exceedingly variable, thus affording important generic and specific characters. It is often corneous and margined with teeth and may terminate in single or paired processes which, in their turn, may be simple, bifid or denticulate. In *Agriotes* this segment is relatively simple and bears a pair of dark-coloured pits possibly sensory in function. The larva of *Cardiophorus* is very different from the prevailing Elaterid type, being extremely long and vermiform, owing to the great development of the intersegments of the abdomen. The 9th segment of the latter region bears a pair of recurved hooks and a terminal fasicule of setæ. Larvæ of certain genera are exceedingly injurious to agriculture and are known as " wireworms " : under this category are species of *Agriotes* (Fig. 505), *Limonius*, *Athous* and others. The " wireworm " group of larvæ are root-feeders and are extremely destructive to pastures, cereals, root crops, etc. (Fig. 504) : no effectual method of control has yet been devised. Other larvæ are lignicolous and xylophagous (*Melanotus*, etc.), or possibly carnivorous (*e g Athous rhombeus*). Exact observations regarding the length of the larval stages are greatly needed : in the case of *Agriotes obscurus*, which is probably the commonest English wireworm, Rymer Roberts considers that the early estimate of five years is approximately correct. This species constructs an earthen pupal cell, and the pupal instar only occupies about three weeks. A large number of Elaterid larvæ have been described by Beling (1883), Henriksen (1911), Hyslop (1917), Schiödte and others: for the metamorphosis of *Agriotes obscurus* vide Ford (*Ann. App. Biol.* 3) and Rymer Roberts (*Ibid.* 6, 8, and 9).

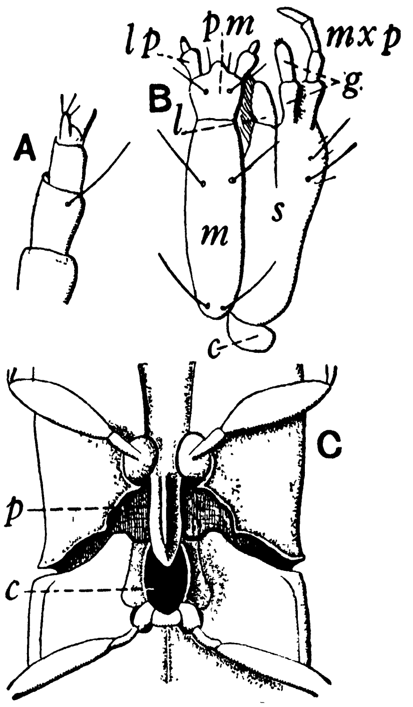

FIG. 504.—ELATERIDÆ.

A, right antenna ; B, labium and left maxilla of *Agriotes* larva. C, base of pro- and mesosternum of *Athous* (adult) showing process *p* and cavity *c* of leaping apparatus , *g*, galea , *l*, lacinia ; *lp*, labial palp , *m*, mentum ; *mxp*, maxillary palp ; *pm*, prementum ; *s*, stipes.

The remaining subfamilies are small and unimportant and are unrepresented in the British fauna. The Cebrioninæ have no power of leaping and the legs are fossorial. The development of *Cebrio gigas* takes place in the ground : its apterous females remain in that situation, protruding the apex of the abdomen, in which position they are fertilized by the males. The Perothopinæ and the Cerophytinæ only include a few species.

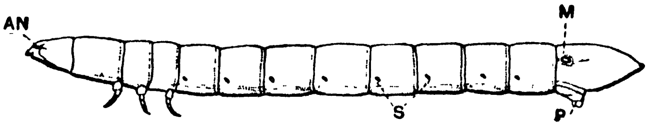

FIG. 505.—LARVA OF *AGRIOTES OBSCURUS*. × 5.

AN, antenna ; *M*, margin of pit : *P*, anal pseudopod ; *S*, spiracles.

FAM. THROSCIDÆ.—SEPARABLE FROM THE ELATERIDÆ ON ACCOUNT OF ANTERIOR COXAL CAVITIES BEING FORMED BY THE PRO- AND MESO-STERNUM. **This small family has been classed with the Eucneminæ but the totally different formation of the anterior coxal cavities separates them. They are small and inconspicuous insects found on flowers, among herbage, at roots of grass, etc. Several species of *Throscus* occur in Britain and very much resemble short Elaterids in form.**

Superfamily III. Heteromera

VENATION OF THE CANTHARID TYPE. ANTENNÆ GENERALLY SIMPLE, MORE RARELY SERRATE, PECTINATE OR FLABELLATE, OR CLUBBED. FORE AND MIDDLE TARSI 5-JOINTED, HIND PAIR 4-JOINTED. TESTICULAR FOLLICLES SESSILE : TWO OR THREE PAIRS OF MALE ACCESSORY GLANDS : USUALLY

SIX, RARELY FOUR MALPIGHIAN TUBES. LARVÆ CAMPODEIFORM, OR MORE USUALLY OF AN INTERMEDIATE TYPE.

This group, as its name implies, is founded upon the tarsal characters, and it includes somewhere between 15,000 and 20,000 species, the great majority belonging to the Tenebrionidæ. The genera comprise a greater diversity of forms than those of any other superfamily and, as Fowler points out, their chief peculiarity lies in the fact that they reproduce nearly all the most characteristic forms of other family-series. In many cases it is difficult to regard the resemblances as cases of mimicry in the true sense of the latter term, and the significance of this convergence is not understood. It has been pointed out by Sharp and others that the larvæ of the Heteromera fall into three groups.

1. Those regularly cylindrical with hard integument and devoid of tubercles or pseudopods. Ex. Tenebrionidæ.

2. Those with a soft integument and of more variable form: tubercles or pseudopods often present on the dorsal and ventral surfaces. Ex. Œdemeridæ.

3. Those with hypermetamorphosis, the young larva being campodeiform but becoming modified in the later instars. Ex. Meloidæ.

Table of the principal families, after Leconte and Horn (1883) and Fowler (1912):

1	(6).—Anterior coxal cavities closed behind.	
2	(5).—Tarsal claws simple.	
3	(4).—Anterior coxæ globose, rarely oval, not prominent: penultimate tarsal joint rarely bilobed and spongy beneath.	TENEBRIONIDÆ (p. 519)
4	(3).—Anterior coxæ conical or conical-ovate, prominent: penultimate tarsal joint nearly always bilobed and spongy beneath.	LAGRIIDÆ (p. 519)
5	(2).—Tarsal claws pectinate.	CISTELIDÆ (p. 519)
6	(1).—Anterior coxal cavities open behind.	
7	(28).—Prothorax without sharply produced or strongly dentate margins: size moderate or small.	
8	(15).—Head not strongly and abruptly constricted at the base.	
9	(14).—Middle coxæ not very prominent.	
10	(11).—Antennæ received in grooves on prosternum.	MONOMMIDÆ (p. 520)
11	(10).—Antennæ free.	
12	(13).—Thorax laterally margined: disk with basal impressions.	MELANDRYIDÆ (p. 520)
13	(12).—Thorax not margined, disk not impressed at base.	PYTHIDÆ (p. 520)
14	(9).—Middle coxæ very prominent.	ŒDEMERIDÆ (p. 520)
15	(8).—Head strongly constricted at base.	
16	(21).—Prothorax at base not narrower than base of elytra.	
17	(20).—Lateral suture of thorax distinct.	
18	(19).—Hind coxæ laminate.	MORDELLIDÆ (p. 520)
19	(18).—Hind coxæ not laminate.	SCRAPTIIDÆ (p. 520)
20	(17).—Lateral suture of thorax absent.	RHIPIPHORIDÆ (p. 520)
21	(16).—Prothorax at base narrower than base of elytra.	
22	(23).—Claws cleft.	MELOÏDÆ (p. 520)
23	(22).—Claws not cleft.	

24 (25).—Antennæ serrate, subpectinate or ramose : head horizontal or almost so : comparatively large insects. PYROCHROIDÆ (p. 521)

25 (24).—Antennæ filiform or moniliform (very rarely flabellate) : head deflexed : very small insects.

26 (27).—Penultimate joint of tarsi minute, concealed : head constricted just behind the eyes which are large. XYLOPHILIDÆ (p. 522)

27 (26).—Penultimate joint of tarsi not minute, bilobed : head constricted at some distance behind the eyes which are small. ANTHICIDÆ (p. 522)

28 (7).—Margins of prothorax dentately produced : size very large. TRICTENOTOMIDÆ (p. 522)

FAM. TENEBRIONIDÆ.—One of the largest families of Coleoptera comprising more than 10,000 species which exhibit an extraordinarily wide range of superficial dissimilarity : the larvæ on the other hand are strikingly uniform in character. Many are ground beetles, usually black in colour, and often bear a superficial resemblance to the Carabidæ. These forms are very often apterous, or have vestigial wings, and the elytra are frequently immovable. Many of the wood-feeding species have ample wings. The species of *Blaps* often occur in cellars and outbuildings. *Tenebrio molitor* and *T. obscurus*, and other species of the genus, are nearly cosmopolitan : they are found in all stages in meal, flour and stored goods, their larvæ being known as "meal worms" (Fig. 506). *Tribolium* has very similar habits and *T. ferrugineum* F. and *T. confusum* are likewise widely spread, through commerce, in granaries and stores (Fig. 507). An account of the biology of *Tenebrio* is given by Cotton and St. George (1929). Species of other genera live in dung, in dead animal matter, in fungi, under bark, etc. The larvæ of this family bear a tolerably close resemblance to those of the Elateridæ, but the labrum is plainly visible and the terminal segment of the abdomen rarely attains the complexity found in that family. For a bibliography of Tenebrionid larvæ vide Gravely (1916).

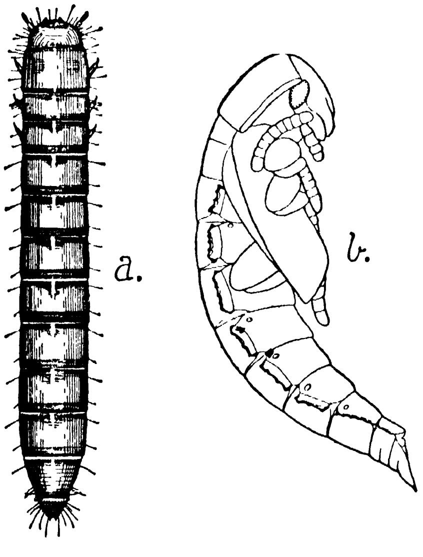

FIG. 506.—*Tenebrio obscurus*, Larva and Pupa : Enlarged.

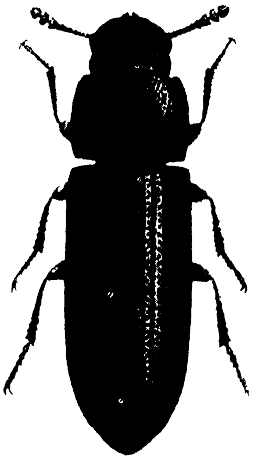

FIG. 507.—*Tribolium ferrugineum*, Cosmopolitan. × 14.

Related to the Tenebrionidæ are three small families of minor importance. The **ÆGIALITIDÆ** include a few minute rare insects from N.W. America and according to Sharp they are allied to the Pythidæ. The **RHYSOPAUSSIDÆ** include a few termitophilous forms : Wasmann (*Zeits. wiss. Zool.* 1912) regards them as a sub-family of the Tenebrionidæ. The **OTHNIIDÆ** include a single genus of arboreal insects found in warm regions of both hemispheres.

FAM. LAGRIIDÆ.—A small family which is closely allied to the Tenebrionidæ and whose members are chiefly found on the leaves of trees and bushes, or under bark. The only British representative is *Lagria hirta* : the larva of this species (vide Schiödte) is somewhat broader and more active than those of the Tenebrionidæ and the segments are furnished with lateral tufts of hairs. The head is very short and the last body-segment is bifid at the apex. The pupa is remarkable on account of the long broad clavate processes which project from most of the abdominal segments.

FAM. CISTELIDÆ.—The pectinate claws appear to be the only feature which separates these insects from the Tenebrionidæ. About 500 species are known : many occur on flowers and their larvæ have been found in dead wood. Five genera are

British and the larva of *Cistela* is described by Westwood (*Classif.* 1, p. 310). The Monommidæ and Nilionidæ are two small extra-European families and nothing is known concerning their biology. The Petriidæ are represented by a few species from the Transcaspian region.

FAM. ŒDEMERIDÆ.—A considerable family of soft-bodied insects bearing a resemblance to the Cantharidæ. They are widely distributed and usually found on flowers or among herbage. They are mostly slender, elongate insects of metallic or other bright coloration. Four genera and six species are British: *Œdemera nobilis* exhibits sexual dimorphism, the male is larger than the female and has greatly thickened femora and tibiæ. *Nacerdes melanura* is a coastal species chiefly found among piles or old cast-up timber. The metamorphoses of several genera are described by Schiödte and the larvæ occur in old wood or under bark. In addition to thoracic limbs, they are usually furnished with dorsal and ventral pseudopods of variable number which aid in locomotion.

FAM. PYTHIDÆ.—This family includes a small number of species which have mostly been found in cold or temperate climates. The British members chiefly occur under bark: *Rhinosomus* has a well marked rostrum, *Pytho depressus* is a rather large flattened insect found in Scotland, and *Salpingus* and *Lissodema* are Carabid-like forms. For the larvæ of *Rhinosimus* and *Lissodema* vide Perris.

FAM. MELANDRYIDÆ.—These insects are mostly found in northern temperate regions where they occur in dry wood and fungi, or under bark: they are represented in Britain by thirteen genera of very diverse forms, and practically all are rare or local. *Osphya* is exceptional in that it is found on flowers and the sexes are very dissimilar. The larvæ are variable and several are described by Perris.

FAM. SCRAPTIIDÆ.—These small delicate insects are mainly found in the palæarctic region. The species of *Scraptia* occur in rotten wood, fungi, etc., and have been relegated by different authors to various families. They are related to both the Mordellidæ and Melandryidæ and are placed by Fowler between those two families. Only two species have occurred in Britain, both rarely. The larva of this genus is described by Perris: it is principally characterized by the great length and spoon-shaped form of the last abdominal segment.

FAM. MORDELLIDÆ.—These beetles are common on flowers and among herbage and some have been found about decaying wood: several of the British species of *Anaspis* are fairly plentiful, especially *A. frontalis*. The metamorphoses of *Mordellistena* are well figured by Riley: the larvæ have been found in the stems of plants under circumstances indicating that they probably prey upon other insect larvæ present. They are elongate and curved, with short legs, and in some species at least there are dorsal prominences on the more anterior abdominal segments. The larva of *Tomoxia* is figured by Schiödte and has been found in decaying wood, while that of *Anaspis* is figured by Perris. In the two latter genera the abdominal prominences are wanting.

FAM. RHIPIPHORIDÆ.—Included in this family are several species of great interest on account of their larvæ being parasites upon other insects. *Metœcus paradoxus* is a parasite in nests of *Vespa*, particularly *V. vulgaris*. According to Chapman (*Ann. Mag. Nat. Hist.* 1870: *Ent. Month. Mag.* 1891), the newly hatched larva is black and campodeiform, resembling that of *Meloë*, but how it enters the nest of its host does not appear to have been ascertained, since the eggs are laid in old wood. Two hypotheses have been put forward—either the eggs are transferred along with wood fragments by the wasps to their nests, or the young larvæ attach themselves to the wasps while the latter are gathering wood. Within the nest the larva becomes an endoparasite of that of *Vespa*: it subsequently becomes an ectoparasite, and gradually devours the whole of its host. Pupation takes place in the cell of the attacked individual, and the adult beetles are found up to the number of twenty or more in a single nest: more rarely they occur on flowers, etc., outside the nest. Among other genera *Emenadia* has a very similar life-history, but utilizes *Odynerus* as its host, while *Symbius* is an endoparasite of Blattidæ: the female is apterous and larviform and does not leave the body of its host.

FAM. MELOÏDÆ (Cantharidæ: Blister Beetles and Oil Beetles).—This family is one of the most interesting of all groups of Coleoptera on account of the remarkable life-histories of its members and the general occurrence of hypermetamorphosis. At least 1,500 species have been described and they are very widely distributed: *Meloë* (vide Fig. 508*b*), *Sitaris* and *Lytta* occur in Britain. The Meloidæ include two sub-families of which the Meloïnæ are ground insects, devoid of hind-wings, and with the elytra frequently much shorter than the abdomen. The Lyttinæ are generally winged and the elytra cover the abdomen; they mostly occur among herbage or on flowers. The female beetles lay a very large number of eggs (often 2,000 to 10,000) which is explainable on the grounds that the subsequent life-history is extremely precarious, and very large numbers of larvæ perish in the first instar. Oviposition takes place in the soil or on the surface of the ground, and the resulting larvæ prey upon the eggs of Orthoptera and aculeate Hymenoptera. In their first instar they are minute, active, hard-skinned, campodeiform larvæ known as triungulins. At this stage they are principally engaged in seeking out their hosts: having discovered the latter, they subsequently undergo ecdysis and change either into soft-bodied, short-limbed eruciform larvæ or, more rarely, into a modification of the campodeiform type known as the caraboid stage. The next succeeding instars differ from the preceding, and the second, or later larva, passes into a resting period when the insect assumes the pseudo-pupal or "coarctate" condition. The latter is followed by a further larval instar which is succeeded by the pupa.

The biology of *Sitaris muralis* has been investigated by Fabre (1857) and Valery-Mayet (1873). The eggs are deposited near the nests of *Anthophora* about August. The newly hatched triungulins remain lethargic and hibernate until spring when they become more active. A certain number succeed in attaching themselves to the hairy bodies of the male bees, which appear earlier than the females. When opportunity allows, they pass to the female bees and so get carried to the nests of the latter. *Anthophora* constructs cells in the ground, in each of which there is a supply of honey and a single egg. When the bee deposits an egg on the honey, a triungulin slips off her body, alights on the egg, and becomes imprisoned in the sealed-up cell. It consumes the contents of the egg, and changes into a fleshy ovoid eruciform larva with vestigial legs. In this instar it feeds upon the honey stored by its host, and subsequently changes into the so-called pseudo-pupal condition within the larval skin. After about one month, a certain number of individuals pass through the subsequent instars and appear as beetles the same year. More usually, they winter in the pseudo-pupal condition and, in spring, assume a second eruciform stage, which differs comparatively little from the earlier one. No food is taken during this period, and the larvæ soon change into ordinary coleopterous pupæ from which emerge the adult beetles.

Riley (1878) has studied the biology of *Epicauta vittata* in N. America. This insect deposits its eggs in parts of the ground frequented by the locust *Caloptenus*. Triungulins emerge in due course, and explore the soil until they discover the egg-capsules of the Orthopteron. Having found the latter, a single triungulin eats its way in and commences to devour the contained eggs. After a few days ecdysis takes place, and the larva passes into the Caraboid or second instar. After about a week, ecdysis again occurs, and the larva becomes curved in shape. From its general body-form this instar is known as the Scarabæoid stage. The succeeding instar is very similar and, when fully grown, the larva deserts the egg-capsule, and changes near by into the pseudo-pupal stage in which it hibernates. In spring it undergoes further changes, and in the sixth instar it is only slightly different from the Scarabæoid stages. From this condition it passes into the pupa and subsequently into the imago (vide Fig. 201).

The life-history of *Meloë* has been partially followed by Newport (1853) and is apparently very similar to that of *Sitaris*. Its triungulins do not appear to exercise much discrimination, and although their hosts are *Anthophora* and *Andrena*, they have often been found attached to other bees and also hairy Coleoptera and Diptera. Large numbers consequently perish through selecting the wrong host, while still greater numbers probably never discover a host at all. The second instar corresponds with Riley's Caraboid stage, although it more closely resembles the Scarabæoid larvæ in general form. In this condition it feeds upon the stored honey, and afterwards transforms into a legless pseudo-pupa. This form moults and the final larval instar is a thick-bodied apodous grub. Space excludes references to the biology of other members of the family, and the student should consult the work of Beauregard (1890) for further information, also that of Milliken (*U.S. Entom. Bull.*, 976).

The "Spanish fly," *Lytta* (*Cantharis*) *vesicatoria*, of southern Europe is rarely found in England. It yields the pharmaceutical product cantharidin (C_{10} H_{12} O_4) which is prepared from the dried insects. The elytra are alone used in pharmacy and contain more of the active principle than the soft parts collectively. Species of *Mylabris* are known to yield a larger amount of cantharidin than *Lytta* and are also used commercially.

FAM. PYROCHROIDÆ (Cardinal Beetles).—A small family allied to the Melandryidæ, but differing in the head being strongly constricted behind the eyes, and in the penultimate tarsal joints being dilated or bilobed. They mostly occur in the northern temperate region, and are usually large insects, brilliant scarlet, or scarlet and black, in colour. The antennæ are frequently deeply pectinate or ramose. The adults are mostly found under bark or in wood where the larval stages are spent: in warm weather they occur among herbage and on flowers. The metamorphoses of *Pyrochroa coccinea* are well figured by Schiödte (Fig. 508): the larva is elongate and flattened with rather long legs and antennæ. The 8th abdominal segment is very long and the 9th is upwardly inclined, terminating in a pair of stout chitinous processes. Only three species occur in the British Isles.

FAM. XYLOPHILIDÆ.—This small family is frequently united to the Anthicidæ and includes about 200 species, very widely distributed, and found mainly in old trees, dead hedges, or occasionally on flowers. Their larvæ are presumably found in decaying wood. *Xylophilus* (*Hylophilus*) is represented in England by three species.

FAM. ANTHICIDÆ.—Many members of this family have the appearance of small Carabidæ while others bear a superficial resemblance to ants. A large number are known, and the British species of *Anthicus* mostly occur in salt-marshes, in heaps of vegetable débris, hotbeds, etc. *Notoxus* is remarkable for its long stout prothoracic horn which is prolonged over the head. The life-histories in this family appear to be unknown.

FAM. TRICTENOTOMIDÆ.—Only a very few species of these large and conspicuous insects are known and their systematic position has been much disputed. In appearance they strongly resemble Lucanidæ or Prioninæ but they exhibit closer affinities with the Heteromera. The curious larva of *Trictenotoma* has been figured by Gahan (*Trans. Ent. Soc.* 1908). The family is confined to the primæval forests of certain of the moister parts of the oriental region.

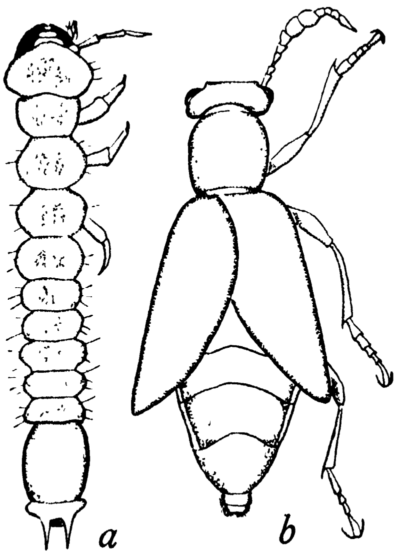

FIG. 508.—HETEROMERA.
a, *Pyrochroa*, Larva; *b*, *Meloe proscarabaeus*, Imago.

Superfamily IV. **Phytophaga**

VENATION OF THE CANTHARID TYPE. ANTENNÆ GENERALLY SIMPLE, LESS OFTEN PECTINATE SERRATE OR DISTALLY THICKENED. TARSI APPARENTLY 4-JOINTED, THE FOURTH JOINT VERY SMALL AND UNITED WITH THE FIFTH. TESTICULAR FOLLICLES ROUNDED AND PEDICELLATE: ONE PAIR OF MALE ACCESSORY GLANDS: MALPIGHIAN TUBES SIX. LARVÆ ERUCIFORM, LEGS SHORT OR RUDIMENTARY, OR ABSENT.

The members of this superfamily are easily recognizable by their tarsal characters, the third joint is either bilobed or dorsally grooved and receives the minute fourth joint at its base (Fig. 509): the first three joints, furthermore, are densely pubescent beneath. Nearly all the 35,000 or more species constituting this group are phytophagous: the Bruchidæ are seed-feeders, the Chrysomelidæ are usually leaf-feeders and the Cerambycidæ are wood and stem feeders. Deviations from this rule are comparatively few but certain members of the last two families are root-feeders. A few exceptions to the structural characters enumerated at the head of this section may be noted. In *Hæmonia* and *Stenopodius* the first three tarsal joints are devoid of the ventral pubescence and the third joint is simple. In certain aberrant Cerambycidæ (Spondylidæ of some authorities) these same features also obtain and the fourth tarsal joint is frequently well developed. In *Donacia*, according to Dufour, there are only four Malpighian tubes and in *Timarcha*, *Melasoma* and a few other Chrysomelidæ the testicular follicles are of the sessile type (Bordas).

Table of families:

1 (2).—Mentum pedunculate. BRUCHIDÆ (p. 523)
2 (1).—Mentum not pedunculate.
3 (4).—Antennæ short or moderate, not inserted on frontal prominences: tibial spurs usually absent. CHRYSOMELIDÆ (p. 523)
4 (3).—Antennæ generally long or very long, frequently inserted on frontal prominences: tibial spurs present. CERAMBYCIDÆ (p. 525)

FAM. BRUCHIDÆ (Lariidæ)—These insects are distinguished from other Phytophaga by the head being shortly and flatly produced and by the stalked mentum. The truncated elytra, which leave the apex of the abdomen exposed, are also very characteristic. The position of the family has often been discussed, many authors having regarded it as being closely related to the Anthribidæ (p. 527) through the genus *Urodon.* As Leconte and Horn observe, the Bruchidæ may be defined as Chrysomelidæ with a pedunculate mentum. Over 700 species are known and their larvæ mostly live in seeds of Leguminosæ, causing great injury to peas, beans, lentils, etc.: those of certain other species attack coco-nuts and palm-nuts. On account of this habit they are very often carried from one country to another in cargoes of seeds. They are frequently, though erroneously, known as pea and bean "weevils." About a dozen species have been found in the British Isles, several being direct introductions from other lands.

The eggs of Bruchidæ are usually laid on the young seed pods, as for example in *Bruchus pisorum*, and the larvæ mine their way through until they reach the seed. In *Pachymerus chinensis* and *Acanthoscelides obtectus* the eggs are laid either upon the pods or the seed, while *Bruchus pruinosus* lays them on the seed. In *B. pisorum* of the pea only a single larva enters a seed and dried peas are unattacked. *A. obtectus* readily attacks dried beans and in suitable climates six generations may occur in the year in the same batch of seed. The larvæ in this family are eruciform and grub-like with thick bodies, becoming curved in the later development when they resemble those of the Curculionidæ. The head is small and often narrower than the prothorax, with short stout mandibles. The first instar differs from those that follow in possessing legs and prominent spinous pronotal processes. In *B. pisorum and B. fabæ* Riley states the legs are slender and 3-jointed, but atrophy once the boring life within the seed is assumed. The retention of these appendages in certain species requires further investigation. Thus, in *A. obtectus* they are similarly present in the first instar, but most writers state that they subsequently atrophy. Razzauti, however, finds that they persist throughout life in the form of papilla-like vestiges. Owing probably to the nutritious nature of the endosperm upon which it feeds, a single larva usually devours only a small amount of nutriment but where many occur in a single seed, as in *A. obtectus,* destruction is more complete. Pupation takes place as a rule within the seed.

FAM. CHRYSOMELIDÆ.—This family competes very closely with the Curculionidæ as regards number of species and probably over 50,000 have been described. They are extremely closely allied to the Cerambycidæ, and there appear to be no definite and constant structural differences separating the two families. As a rule, the Chrysomelidæ are very different in general appearance: their antennæ are only of moderate length, and the eyes do not embrace their points of insertion: the upper surface of the body is generally bare and shining, frequently with metallic coloration. Jacoby ("*Fauna of India*") adopts six primary divisions of the family according to the following key.

1 (8).—Mouth placed anteriorly.
2 (7).—Antennæ widely separated at base; elytra of hard texture.
3 (6).—Intermediate ventral segments not medially constricted; pygidium not exposed.
4 (5).—Thorax without distinct lateral margins, head produced, eyes prominent, prosternum exceedingly narrow. EUPODA
5 (4).—Thorax with distinct lateral margins (rarely without), head not produced, eyes not prominent, prosternum broad. CYCLICA
6 (3).—Intermediate ventral segments constricted; pygidium usually exposed. CAMPTOSOMES

7 (2).—Antennæ not widely separated at base, generally closely approximate; elytra more or less soft in texture. TRICHOSTOMES
8 (1).—Mouth not normal, small, hidden or nearly so. CRYPTOSTOMES

The Eupoda include the Sagrinæ, Donaciinæ and Criocerinæ. The Sagrinæ are large brilliantly coloured tropical insects with strongly thickened hind femora. Only two species are European and both are rare in Britain. According to Sharp the larva of *Sagra splendida* lives in swellings on the stems of *Dioscorea*. The Donaciinæ are elongate and usually metallic insects common in temperate climates. They are aquatic in the pre-imaginal stages and in *Hæmonia* the adults also live beneath the water. The metamorphoses of *Donacia* have been investigated by Schmidt-Schwedt (*Berlin Ent. Zeits.*, 1887, 1889), MacGillivray (1903), Boving (1910), and others. The larvæ feed submerged at the roots or in the stems of water plants. They are elongate, sub-cylindrical whitish creatures with short, hooked thoracic legs. The abdomen is terminated by a pair of spinous processes, the structure and functions of which have been much discussed. They enable the insect to perforate the plant tissues and insert its caudal extremity into the air spaces for purposes of respiration. When feeding, they gnaw holes in the plants and, by means of their specially modified mouth-parts, they extract the sap which is pumped into the digestive system by the aid of the pharynx. The pupæ are enclosed in tough cocoons attached to the roots of the host plants. The Criocerinæ are represented in Britain by a few species of *Zeugophora*, *Lema* and *Crioceris*. Their larvæ are short, thick, fleshy grubs which feed externally on the leaves of plants. Some have the habit of concealing themselves with coverings of excrement while other, and often closely allied species, do not possess this trait. The asparagus beetle (*Crioceris asparagi*) is familiar to growers of that vegetable, and *Lema melanopa* is occasionally injurious to growing cereals.

The Cyclica include the greater number of the species of the family and over 170 are British (Fig. 509). Their larvæ live exposed on plants and are short and convex, frequently with leathery pigmented integument: those of *Orina* are well figured by Chapman (1901, 1903) and of *Leptinotarsa* by Tower (1906). The latter genus includes the well known Colorado potato beetle (*L. decemlineata*). The larvæ and imagines of *Phædon* are destructive to Cruciferæ, particularly mustard, the former feeding in companies on the leaves. According to Chapman (1901) certain species of *Orina* are viviparous and this same method of reproduction is recorded by Williams (*Entom.* 1914) in *Phytodecta viminalis*.

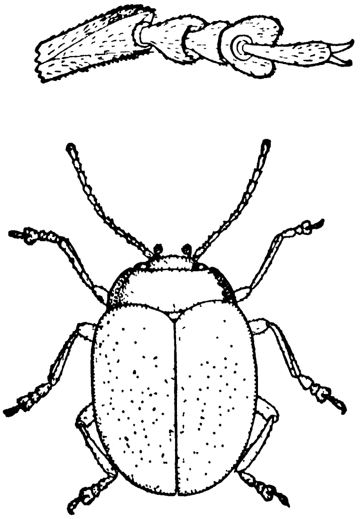

FIG. 509.—*CHRYSOMELA STAPHYLEA*. EUROPE AND N. AMERICA. × 4. ABOVE—TARSUS MORE HIGHLY MAGNIFIED.

The Camptostomes are characterized by the peculiar structure of the abdomen which appears to be correlated with the formation of a case which envelops the egg. The larvæ are also enclosed in cases which are composed, at least partially, of excrement. Owing to their concealed life they are usually devoid of pigment and resemble small Scarabæid larvæ in general form. The larval cases of *Cryptocephalus* and *Clythra* are described by Weise, Fabre and others: in the former genus they are carried almost erect and the larvæ move with a jerky action. The life-history of *Clythra quadripunctata* has been studied by Donisthorpe (*Trans. Ent. Soc.*, 1902): its larvæ live in nests of *Formica rufa* and their cases are composed of a mixture of earth and excrement.

The Trichostomes include the Galerucinæ (Fig. 510) and Halticinæ, both sub-families comprising a number of highly injurious species. Their larval habits are extremely varied: many feed openly on the parenchyma of leaves, others live in roots, and a considerable number are leaf-miners. The turnip flea beetle, *Phyllotreta nemorum*, and other members of the genus, are exceedingly destructive to Cruciferæ, especially to the turnip. This genus and other members of the Halticinæ have greatly developed leaping powers which reside in the swollen hind femora.

The Cryptostomes consist of the Hispinæ and Cassidinæ. The species of *Hispa* are usually covered with long stout upright spines: they are mainly tropical and their sub-family is unrepresented in the British fauna. Their larvæ so far as known are leaf-miners. The Cassidinæ include the " tortoise " beetles, and have the lateral margins of the body greatly expanded which give these insects a flattened shield-like appearance. Many are notable for their extremely brilliant coloration which fades very quickly after death. Their metamorphoses are of a remarkable character (vide Muir and Sharp, 1904) : in certain species the eggs are enclosed in an ootheca often of complex structure, in others the ootheca is very small and imperfect and a layer of excrement is laid over it. The larvæ are short and oval, somewhat flattened and spiny, often assuming bizarre forms : they usually cover their bodies with excrement which is supported and attached by a forked caudal process. The cast skins also form part of this adventitious covering, and the excrement may either form a solid pad, attached to the exuviæ, or assume the condition of long filaments.

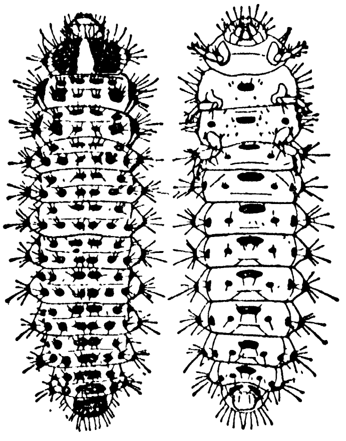

FIG. 510.—*GALERUCELLA LUTEOLA*, LARVA, DORSAL AND VENTRAL ASPECTS. ENLARGED.

After Silvestri.

FAM. CERAMBYCIDÆ (Longicornia).—The longicorn beetles number about 13,000 species mostly of elongate form and attractive coloration (Fig. 511) Some of the members, such as *Macrotoma heros* and *Titanus giganteus*, are among the largest of insects. The family exists throughout the world wherever there is woody vegetation, and includes an almost infinite variety of shape and ornamentation among its species. Although frequently dissociated into two or three divisions, each of separate family rank, it is scarcely necessary for general purposes to do otherwise than follow Sharp and regard these insects as forming a single family. The number of genera and species found in Europe is very small compared with those of the tropics. Only a few outlying representatives of this extensive group occur in Britain, and they comprise about 65 species, several being exceedingly rare or doubtfully indigenous. A number of forms are well known for their cryptic coloration, while others exhibit a close mimetic resemblance to insects of other families and also of other orders. One of the most striking cases of cryptic coloration is afforded by the African *Petrognatha gigas* whose whole upper surface resembles dead velvety moss and its irregular antennæ are very like dried tendrils or twigs. The common British species *Clytus arietis* bears a close resemblance to *Vespa* : it, furthermore, runs actively and exhibits antennal movements highly suggestive of those of a wasp. An interesting digression on these subjects will be found in the work of Fowler (1912) where a number of instances are enumerated. Many Cerambycidæ possess the faculty of stridulating : in some cases the sound is caused by the hind margin of the prothorax working against a specialized striated area at the base of the scutellum : in others sound is produced by the friction of the hind femora against the edges of the elytra. In the Hawaiian *Plagithmysus* both types of organs are present in the same insect.

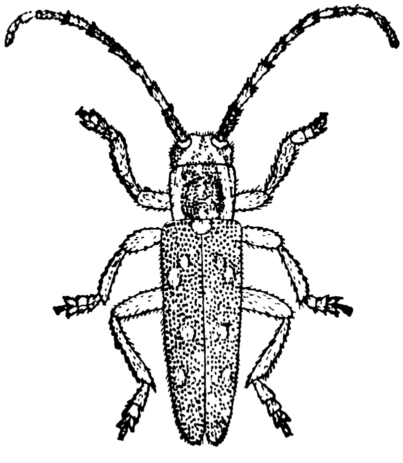

FIG. 511.—*SAPERDA POPULNEA*, EUROPE AND N. AMERICA. × 2.

The larvæ of the Cerambycidæ bore for the most part into the wood of trees; but a few are confined to the roots or pith of herbaceous plants. Most species affect dead or decaying trees, some selecting moist and others dry wood. Certain species bore into the bark or into the sap or heart-wood of living trees and a few, such as *Saperda*, live in stems. The pupal habits are likewise varied, this instar occurring in the wood, between the latter and the bark, or in the bark. The pupa lies in the final larval burrow or in a special gallery leading therefrom and, in either case, a closed chamber is formed by the entrance being plugged with frass or fibrous chips. Many species adopt further measures for sealing up the pupal chamber (vide Beeson

Ind. Forest Bull. 38, 1919). In these cases a large amount of calcium carbonate is produced by the Malpighian tubes, this substance being mixed with gummy or silky matter and utilized for constructing an operculum which completely closes the pupal cell. In other cases the whole of the latter may be lined by an egg-shell-like coating of the same substances. Cells which are closed or lined in this manner are protected from various enemies and are also probably enabled to maintain the requisite moisture-content. On account of their concealed mode of life, the larvæ (Fig. 512) are soft and fleshy and of a whitish or yellowish colour: they are, furthermore, often finely pubescent. The form of the larvæ is largely correlated with their habits, the bark-boring species being more or less flattened while those living in wood or stems exhibit a tendency to become cylindrical. The head is invaginated into the prothorax and is usually small and transverse, but in the Lamiinæ it is longer than broad. The prothorax is large and is broader than the remaining trunk-segments. The 9th abdominal segment is often longer than those preceding and somewhat vesicular: in the Aseminæ it bears a pair of chitinous spines. Thoracic legs are generally present, but are usually so much reduced as to be non-functional: in most of the Lamiinæ they are wanting. Locomotion takes place by the aid of dorsal and ventral segmentally arranged abdominal swellings which, in some genera, bear chitinous asperities. In many larvæ a variable number of the anterior abdominal segments bear small asteriform structures known as pleural discs which are the points of attachment of chordotonal organs (vide p. 90).

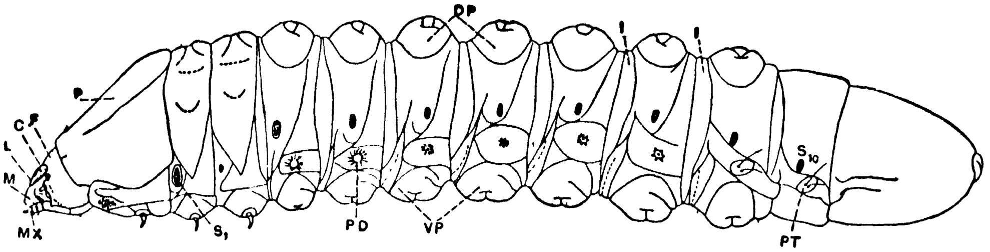

Fig. 512.—Cerambycidæ: Lateral View of a Typical Larva.

C, clypeus; *DP*, dorsal pseudopods; *F*, frons; *I*, intersegmental region; *L*, labrum; *M*, mandible; *MX*, maxilla; *P*, pronotum; *PD*, pleural disc; *PT*, pleural tubercle; S_1, 1st thoracic spiracle; S_{10}, 8th abdominal spiracle; *VP*, ventral pseudopods. Adapted from Craighead *U.S. Dept. Agric. Office of Sec. Report*, 107.

The writings of Perris and Schiödte include descriptions of a number of larvæ belonging to this family, while among more recent works those of Craighead (*Dept. Agric. Canada, Bull.* 27 *n.s.*) and Kemner (*Ent. Tidskr.* 43, 1922) should be consulted. Among life-history studies those of Ritchie (1920) on *Saperda* and Crawshay (*Trans. Ent. Soc.* 1907) on *Tetropium* may be mentioned. In *Saperda carcharias* the life cycle occupies about four years in Scotland, the first winter being passed in the egg stage. In *Tetropium gabrieli*, on the other hand, the life-history is of one year's duration and hibernation occurs in the larval stage. The shorter cycle is more usual, but the relative supply of moisture and the nutrient qualities of the food tend to increase or diminish the normal time by months or even years. Several instances are recorded in which wood, made into furniture many years, has been found to contain larvæ which finally emerged as imagines (Craighead).

Superfamily V. **Rhynchophora**

VENATION OF THE CANTHARID TYPE BUT OFTEN MUCH MODIFIED AND APPROXIMATING TO THE STAPHYLINID TYPE. HEAD GENERALLY PRODUCED INTO A ROSTRUM; GULAR SUTURES CONFLUENT: ANTENNÆ STRAIGHT, OR GENICULATE AND CLAVATE. PLEURO-STERNAL SUTURES OF PROTHORAX WANTING: TARSI APPARENTLY 4-JOINTED. TESTICULAR FOLLICLES ROUNDED AND PEDICELLATE: MALE ACCESSORY GLANDS VARIOUSLY DIFFERENTIATED: MALPIGHIAN TUBES SIX. LARVÆ ERUCIFORM, USUALLY APODOUS.

The Rhynchophora are a highly organized and much modified group, and the theory once held that they represent the lowest type of Coleoptera is now regarded as untenable. Their nearest affinities are with the Phytophaga and, according to Ganglbauer, they were probably derived from them through the Bruchidæ. As is pointed out by Gahan, there are a few genera in which the gular sutures are distinct and separated, viz. *Rhinomacer* and *Oxycorynus*, in the Curculionidæ, and in some Scolytidæ, as for example *Crossotarsus*. In the vast majority of the Rhynchophora, however, the gula is wanting and there is only a single median suture or even the latter may be absent. The pleuro-sternal sutures on the prothorax are present in *Rhinomacer* and its allies, and traces may be observed near the coxæ in many genera of Curculionidæ (Marshall). With very few exceptions, the prosternal epimera are fused in the middle line behind the coxæ except, according to Marshall, in the Curculionid sub-family Byrsopinæ. In a few cases the tarsi are apparently 3-jointed (Aglycyderidæ and Proterhinidæ) and they are very rarely 5-jointed. In the Scolytidæ and many Anthribidæ there is no distinct rostrum. The larvæ in this superfamily are phytophagous, feeding upon almost all parts of the plant including the wood, bark, and roots. Those of the Brenthidæ and certain of the Anthribidæ possess reduced legs, but for the most part they are apodous.

Table of the families (partly from Marshall):

1 (2).—Palpi normal, flexible: labrum distinct: pronotum with lateral margins carinate. ANTHRIBIDÆ (p. 527)
2 (1).—Palpi very short and rigid: labrum absent or concealed: lateral margins of pronotum not carinate.
3 (6).—Head with a rostrum, at least in female: tibiæ never denticulate externally.
4 (5).—Antennæ rarely clavate and never geniculate: narrow elongate insects. BRENTHIDÆ (p. 527)
5 (4).—Antennæ clavate and usually geniculate, but often straight. CURCULIONIDÆ (p. 528)
6 (3).—Head never with a rostrum: tibiæ denticulate externally. SCOLYTIDÆ (p. 529)

FAM. BRENTHIDÆ.—A group of elongate narrow insects numbering about 800 species which are almost entirely confined to tropical countries. The size of the individuals of a species is often subject to a great range of variation and the males are usually much larger than the females. In many species the two sexes are structurally very different (Fig. 513). In such instances the mandibles of the male are very large and prominent and the rostrum broad and rudimentary. The females have minute jaws, but the rostrum is very slender, often equalling or exceeding the body in length. The early stages, so far as is known, are passed in wood, and the rostrum of the female is used for boring holes in which the eggs are laid. The larvæ are very little known but are quite different from the usual Rhynchophorous type, being elongate and slender, and provided with thoracic legs. The adults of one or two genera have been observed to be predaceous upon wood-boring insect larvæ. In some genera the antennæ are clubbed, but the joints are quite separate, and not compact as in the Curculionidæ.

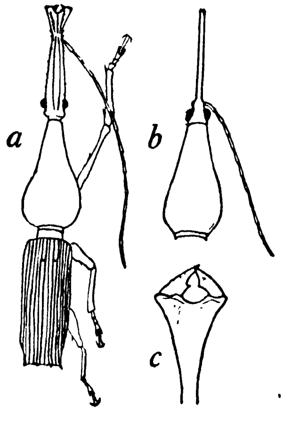

FIG. 513.—*a*, *Ectocemus cinnamonii*, MALE, BORNEO; *b*, HEAD AND THORAX OF FEMALE; *c*, *Euctrachelus*, SUMATRA, EXTREMITY OF HEAD OF MALE.

FAM. ANTHRIBIDÆ (Platyrrhinidae).—This family is very largely tropical and less than a dozen species have been found in the British Isles. Its species are chiefly met with in old wood, dead branches and in fungi, but *Brachytarsus* is exceptional in that it preys upon Coccidæ. *Xenocerus* and other genera have very elongate antennæ and closely resemble Cerambycidæ. The larvæ of several genera are described by Perris: they bear a general resemblance to those of the Curculionidæ except that legs are present in some cases or replaced by tubercles in others.

FAM. CURCULIONIDÆ (Weevils).—The Curculionidæ form the largest natural family in the animal kingdom. Sharp has estimated that 200,000 is the minimum number for the existing species, of which between 60,000 and 70,000 are described. The majority of these insects are characterized by the pronounced rostrum, geniculate clubbed antennæ, and reduced rigid palpi (Fig. 514). A certain number of exceptions are known: thus, in the Rhinomacerinæ the palpi are long and flexible and the labrum is distinct, while in a few Australian genera the rostrum is so short as to be almost absent. In *Dryophorus* the tarsi are 5-jointed. The function of the rostrum in the female is often that of a boring instrument, a hole being drilled by it for placing the eggs: in some species the eggs are inserted far into holes previously made by the ovipositor, but whether the rostrum plays any part in this act or not is uncertain: in a number of cases it is evidently not used for either of these purposes and its function is not understood. The significance of the rostrum in the male appears to be totally unknown. In many instances this organ exhibits sexual differences, being better developed in the female than in the male. This dimorphism is well exhibited among British weevils in *Rhynchites* and *Balaninus*: the S. African *Antliarrhinus* oviposits in cones of cycads and, in the female, the rostrum is about three times the whole length of the body and six times the length of the corresponding organ in the male. The presence of scrobes for the reception of the antennæ, and of provisional pupal mandibles in certain genera, have already been referred to (p. 479). Unlike other Coleoptera, an exceptionally large proportion of the species are clothed with scales, but very little attention has been devoted to their form and structure. As a rule, weevils are of sombre coloration. Exceptions are found in the Rhynchitinæ whose integument exhibits metallic colours: in the brilliant green *Phyllobius* and *Polydrusus*, so common in Britain, the colour is a property of the scales. The Papuan *Eupholus* is sky-blue and the brilliancy of this colour even rivals that of the Lycænidæ. The diamond beetles (*Cyphus* and *Entimus*) of Brazil are probably the most resplendent of all Coleoptera. In some weevils the colour is produced by a fine powdery exudation which is readily abraded and, in a few cases at least, it is stated to be renewed during the life of the insect.

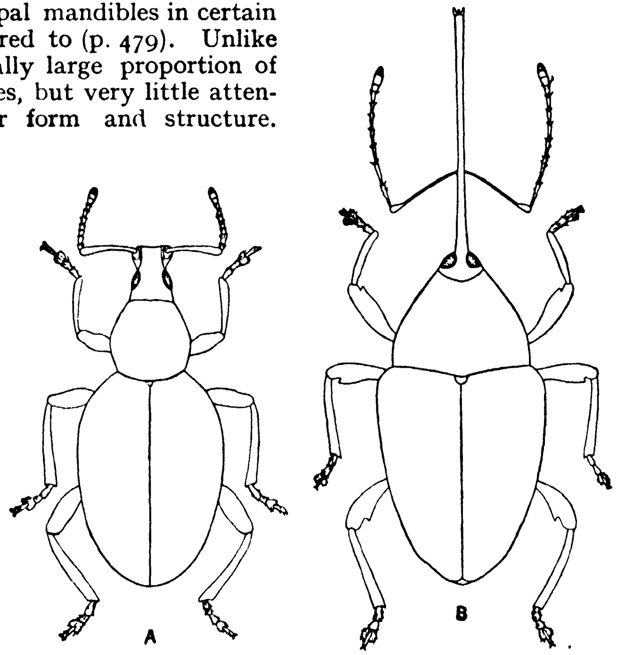

FIG. 514.—A, *OTIORRHYNCHUS PICIPES*. × 6. B, *BALANINUS NUCUM*. × 10.

The larvæ of Curculionidæ are apodous and exhibit great similarity of form. The body is more or less distinctly curved and stout, only slightly narrowing towards the caudal extremity. The head is rounded, exserted, and of a testaceous colour: the rest of the body is greyish or whitish, with a soft furrowed integument. The antennæ are usually reduced to small papillæ and, except in larvæ which are external feeders, there are no ocelli. The vast majority are internal or subterranean feeders, and no part of the plants, from the roots to the seed, is entirely free from the attacks of one or more species. In those larvæ which mine stems or leaves, the body is generally somewhat hairy with locomotory swellings. Such larvæ do not exhibit the curved form prevalent in this family and are often narrowed posteriorly. A few genera are aquatic, their larvæ inhabiting the submerged parts of water plants. The imagines of such genera as *Bagous*, *Eubrychius* and *Litodactylus* are likewise aquatic and the two first mentioned swim by means of the hind-legs. A certain number of genera including *Hypera*, *Cionus* and *Phytobius* feed openly, and in both *Hypera* and *Cionus* the larvæ maintain their position on the plant by means of a viscous secretion which envelops the body. The larvæ of *Rhynchites*, *Attelabus* and *Apoderus* live in tunnels formed of rolled leaves constructed by the adults: an interesting account of these structures in *Deporaus* (*Rhynchites*) *betulæ* is given by Sharp (*Ins.* pt. II). In *Hylobius*, *Pissodes* and *Rhynchophorus* the larvæ tunnel in tree-trunks, more particularly of Coniferæ. Many of the Otiorrhynchinae, *Sitones*, etc., affect roots, while the various species of *Apion* attack the stems, leaves, flowers and seed. *Calandra* is entirely a seed feeder, and species of other genera (*Nanophyes*, *Gymnetron*, *Ceuthorrhynchus*, etc.) form either stem or root galls. When about to pupate, certain species construct cocoons from a product of the Malpighian tubes which is worked up by means of the larval mouth-parts (vide Knab, 1915). It exudes from the anus, and forms the reticulate cocoons of *Hypera*, the parchment-like capsules of *Cionus*, the chalky nodular cocoons of certain species of *Larinus*, and the felted cocoons of *Orchestes*. In the two first mentioned cases the material is the same as that which enveloped the larvæ (vide above). Labial spinnerets occur in some weevil larvæ, and it is likely that the latter may spin cocoons in the strict sense of that operation, or contribute material from stomodaeal glands to the cocoon-forming substance. A large number of Curculionid larvæ pupate in the soil, but on the other hand, many others complete their transformations within the larval food-plant.

Parthenogenesis is known to occur in several species of *Otiorrhynchus*, the discovery being made by the Russian entomologist Silantjev in 1902. This observer found that 1,000 examples of *O. turca* collected at random proved to be all females and individuals were reared subsequently from unfertilized eggs (*Zool. Anz.* 29, 1906). Vassiliev (*Ibid.* 34, 1909) has demonstrated the same phenomenon in *O. ligustici* and Grandi (*Boll. Lab. Zool. Portici* 7, 1913) in *O. cribricollis.*

In a family of the size of the Curculionidæ it is scarcely remarkable that a number of the species are highly injurious, either as larvæ or as imagines also. The granary weevil (*Calandra granaria*) deposits its eggs in the grains of maize, wheat or barley and has become widely distributed through commerce. The cosmopolitan rice weevil (*C. oryzæ*) affects a great variety of food substances including rice and other cereals, dried peas and beans, flour, meal, etc. *Anthonomus grandis* is the Mexican cotton boll weevil—the most serious enemy of the cotton crop in America, where it is estimated to destroy an equivalent of 400,000 bales annually. It is a comparatively recent introduction, having entered Texas about 1892 from tropical America. The eggs are laid in cavities made in the flower buds which usually fail to develop. Under suitable conditions the whole life-history only occupies two to three weeks. *Anthonomus pomorum* is the apple-blossom weevil, locally destructive in many parts of England. It is univoltine and the eggs are laid in the unopened blossom buds. The larvæ feed upon the inner parts of the flower and on the receptacle: growth of the flower ceases, the petals dying and forming a kind of brown cap, hence the name of "capped blossom" for this affection of the tree. *Rhynchophorus ferrugineus* F. is the palm weevil, which infests the toddy and cocoa-nut palms. The eggs are laid in the soft tissue at the bases of the leaf-sheaths, in wounds, or in cuts made by the toddy drawer. The larvæ tunnel the stems in all directions and pupate in fibrous cocoons. *Hylobius abietis* is extremely injurious to young conifers: the weevils gnaw the bark and cambial layer, thus reducing or stopping the flow of sap. The larvæ, on the other hand, are not injurious and mostly live below ground in the roots of trees that have been felled. Certain species of *Apion* and *Sitones* are pests of leguminous crops, and the larvæ of *Ceuthorrhynchus pleurostigma* form conspicuous galls on the roots of cabbages and swedes.

The literature on the structure and biology of members of this family is not extensive, as very few species have been studied in any detail. General introductions to the family and its classification will be found in the works of Blatchley and Leng (1916) and Marshall (1916): from the morphological standpoint, Hopkins' study of the larval and imaginal structure of *Pissodes* (1911) is valuable. For life-history studies those of Trägårdh (1910) on *Orchestes*, Jackson (1920–22) on *Sitones* and Silvestri on *Cœliodes* (*Boll. Lab. Zool. Portici*, 12, 1917), may be mentioned.

FAM. SCOLYTIDÆ[1] **(Ipidæ**: Bark beetles).—These insects are for the most part small and cylindrical, and are well adapted for a concealed life within vegetable tissues (Fig. 515). The majority of the species bore into the bark and between the latter and the wood: others may attack the roots, twigs or solid wood, while still other species attack shrubs and a few select herbaceous plants. A small number of species bore into the fruit or seed of palms, etc., young fir cones, or the wood of casks and barrels. The larvæ and adults feed upon the starches, sugars, and other substances found in the host plants, or upon fungi which grow in the brood galleries. Owing to the habits mentioned above these insects are among the most serious enemies the forester has to contend with. The method of attack is first to construct an entrance tunnel through the bark which, in the wood-boring forms, is carried deeply into the tree: in the bark-feeding species it does not reach further than the surface of the wood. From the inner end of the entrance tunnel two or more egg-tunnels are cut vertically, transversely, or radially between the bark and wood (Fig. 516). With many species a nuptial chamber is excavated at the end of the entrance tunnel and, in such cases, the egg-tunnels originate from it. In most species this chamber is probably constructed by the male. The eggs are laid in niches along the walls of the egg-tunnels and the larvæ excavate slender mines or larval burrows usually at right angles to them. The larval burrows are generally filled with excrement and their calibre increases as the larvæ grow. The form and arrangement of the egg-galleries and larval burrows exhibit various features characteristic of each species or group of species and consequently these excavations are of particular taxonomic value. The extremities of the larval burrows are widened to form the pupal cells, and the adult beetles finally construct exit burrows leading from the pupal cells to the exterior. "Ventilating burrows" are also often constructed: they are located in the roof of an egg gallery and extend to or near the exterior of the tree. Although perhaps serving for ventilation in some cases, they appear to serve more usually for the storage of boring dust, or as an opening through which this material may be ejected.

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[1] Including the Platypodinæ which are often regarded as a separate family on account of the broad head and slender first tarsal joint.

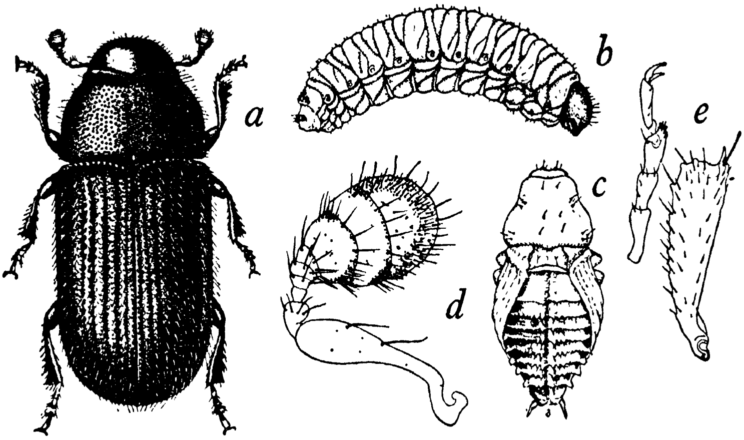

FIG. 515.—SCOLYTIDAE.

a, *Dendroctonus*; *b*, larva; *c*, pupa; *d*, *Gnathotrichus*, antenna; *e*, hind tibia and tarsus. (*a*, *b*, *c* *after* Hopkins. *d*, *e* after Schedl).

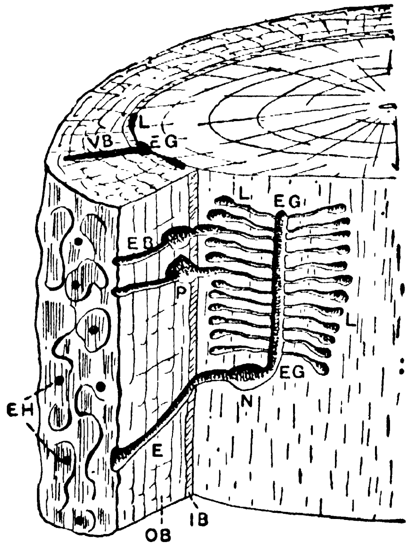

FIG. 516.—SCHEMATIC FIGURE ILLUSTRATING THE TUNNELLINGS OF A BARK BEETLE IN A BRANCH OF A CONIFER.

E, entrance burrow; *EB*, exit burrow; *EG*, egg-gallery; *EH*, exit holes; *IB*, inner bark; *L*, larval galleries; *N*, nuptial chamber; *OB*, outer bark; *P*, pupal cell; *VB*, ventilating burrow.

The social habits and relations of the sexes in this family are of a remarkable nature. As Hopkins remarks, there is a wide range of variation from simple or unorganized and intensive polygamy to specialized or organized polygamy, and a gradual reduction in the number of females associated with a single male from one male and sixty or more females (*Xyleborus*), to one male and two females (*Ips*) and finally to specialized monogamy (*Scolytus*). With many species copulation takes place on the bark of old trees or after alighting on the new host tree. Monogamous species often pair in the entrance tunnel and polygamous species in or near the nuptial chamber.

The ambrosia beetles penetrate the wood and their larvæ are nourished by certain fungi which develop upon the walls of the burrows. A carefully prepared bed or layer of chips and excreta is provided by the female beetle, upon which the fungus develops—ambrosia being the name applied to this fungus-food. The mycelium spreads to the various galleries staining them dark brown or black owing to the action of the fungus upon the wood. Certain species of fungi appear to be associated with individual species of beetles. Unless eaten off regularly, the fungus develops and spreads rapidly and during wet weather it may block up the galleries and kill the occupants. The transportation of the reproductive bodies of the fungus from one tree to another has received diverse explanations and takes place, either fortuitously or intentionally, through the agency of the beetles themselves. In the case of *Xyleborus* it has been stated that the conidia are either voided in the excreta or carried in the crops of the female beetles, and regurgitated when a fungus-bed is being prepared. In other cases it has been found that the brushes on the front of the head in the female of certain species retain the conidia among their hairs, and facilitate transportation. In *Diapus furtivus* Beeson (*Ind. Forest. Rec.* 6, 1917) has observed the same method of conveyance. He also states that groups of large prothoracic pores are found in many Platypodinæ and are each filled with a globule of fatty secretion to which the spores (conidia ?) readily adhere. He has observed the latter germinating *in situ* but they speedily become separated from the insect once the latter is established in its tunnel. Among the best known genera of ambrosia beetles are *Xyleborus*, *Trypodendron*, *Crossotarsus*, *Diapus*, and *Platypus*.

Scolytid larvæ are apodous and usually closely resemble those of the Curculionidæ. The literature on the family is very extensive; among the more important contributions are those of Hopkins (1909, 1915), which are accompanied by a full bibliography, and the writings of Hagedorn, Swaine, Nusslin, Fuchs, etc.: works on forest entomology should also be consulted. Over 1,300 species are known and more than 40 occur in the British Isles.

In addition to the four families already dealt with, the **PROTERHINIDÆ** are a very small and highly aberrant family consisting of two genera. *Aglycyderes* occurs in the Canary Islands and New Zealand and *Proterhinus* inhabits the Hawaiian and other Pacific Islands where it is represented by many species, found under bark, etc.

Superfamily VI. **Lamellicornia**

VENATION OF THE CANTHARID TYPE OR APPROXIMATING BY REDUCTION TO THE STAPHYLINID TYPE. ANTENNÆ WITH A HIGHLY DIFFERENTIATED LAMELLATE CLUB. LEGS USUALLY FOSSORIAL; TARSI 5-JOINTED, FIRST PAIR SOMETIMES WANTING. TESTICULAR FOLLICLES ROUNDED AND PEDICELLATE, AND ALMOST ALWAYS ONE PAIR OF MALE ACCESSORY GLANDS: MALPIGHIAN TUBES FOUR. LARVÆ FLESHY AND CRESCENTIC, OCELLI GENERALLY WANTING, LEGS RATHER LONG.

The Lamellicornia form one of the best defined and most easily recognized of the major divisions of Coleoptera. They have no transitional forms connecting them with other groups, and are regarded by Ganglbauer as being the highest series of the order. They are primarily fossorial, and the burrowing habit persists to a greater or less degree in the majority of the species. In form they are compact and very stoutly built; they are endowed with remarkable muscular powers but they walk without much agility, and in an ungainly fashion. Nearly all species, however, are active fliers: apterous forms are relatively few and, although most frequent in the female, they may occur in both sexes. In some members of the group the colours are bright and striking, and the head and thorax are often ornamented with remarkable cuticular outgrowths, producing some of the most bizarre forms in the insect world. Sexual dimorphism is a very characteristic phenomenon, the differences affect almost every part of the body and, in many cases, the males and females of a species are so unlike that they have been relegated to different genera (Fig. 460). Lamellicornia are also remarkable for the variety of their stridulating organs, not only in the imagines, but more particularly among the larvæ: the sound produced is usually very highly pitched, and often inaudible to the human ear, if the insect be held more than a few inches distant. The eggs are large and few in number: they are noteworthy from the fact that they have been observed to change considerably their form and size during growth after deposition. During the larval stage these insects feed upon dead vegetable or animal matter, roots, or dung and occur in the ground, in the decaying parts of trees, or in débris, etc. The larvæ are described by Schiödte, Perris and others. They are easily recognized and exhibit great similarity. They are broad and fleshy, whitish or greyish white and the body is curved in the form of a letter C; the legs are well developed, but are rarely used for locomotion. The majority of species lie upon the back or side and are surrounded by sufficient food to render active movement unnecessary. The head is large and downwardly inclined and strongly chitinized; the three thoracic segments are short, bringing the legs closely together, and the last two to four abdominal segments have a somewhat inflated appearance being much larger than those preceding. Eyes are seldom present, but the antennæ are well developed and 2- to 5-jointed. The mandibles are powerful and exposed, and the maxillæ terminate either in one or two lobes. The prothorax and first eight abdominal segments each bear a pair of spiracles.

A general account of the Lamellicornia is given by Arrow (1910); they are divided into three families which may be recognized by the following characters:

1 (4).	—Antennæ not elbowed.	
2 (3).	—Joints of antennal club not very thin, brought together by rolling up.	PASSALIDÆ (p. 532)
3 (2).	—Joints of antennal club very thin, closely coadapted and incapable of being rolled up.	SCARABÆIDÆ (p. 533)
4 (1).	—Antennæ almost always elbowed, the joints of the club not very thin or coadapted.	LUCANIDÆ (p. 532)

FAM. PASSALIDÆ.—The members of this family are somewhat flattened, black or dark brown insects. The elytra (Fig. 517*a*) cover the abdomen and are deeply longitudinally striated, and the mandibles are not specially developed in the male. About 250 species have been described and they inhabit decaying wood in the moist warm forests of the world. None are European, and only a single species occurs in America north of Mexico. These insects appear to have attained a degree of social organization that is quite exceptional among Coleoptera. Ohaus has observed the two parent beetles accompanied by several larvæ which they tend throughout life until maturity is attained. The adults disintegrate the wood and chew it into a condition suitable for consumption by their progeny. The larvæ (vide Gravely, 1916) are more elongate and less markedly crescentic than those of most Lamellicornia (Fig. 519). They are, furthermore, active and have the first two pairs of legs relatively long: the third pair are greatly modified, each leg being reduced to a very short coxa and a more elongate trochanter. The latter is adapted to form an organ which works across a striated area on the mesocoxa, thus producing a squeaking noise. Stridulation is effected in the adults by friction between the wings and the upper surface of the abdomen.

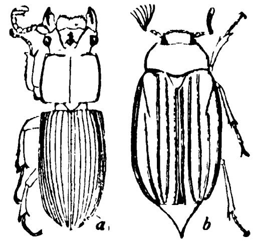

FIG. 517.—*a*, *Passalus interruptus*, Paraguay; *b*, *Melolontha vulgaris*, Britain.

FAM. LUCANIDÆ (Stag beetles).—In these insects the abdomen is covered by the elytra but the latter are almost always devoid of longitudinal striæ. Stag beetles are familiar on account of the great development of the mandibles in the males which in some cases attain a length equal to that of the rest of the body (Fig. 518). The significance of these enormous mandibles is not clear: notwithstanding their formidable appearance in *Lucanus cervus*, for example, they are not as strong, or as capable of inflicting as severe a bite, as the short stout mandibles of the female. The male insects are usually much larger than those of the other sex and they exhibit great variation in size among individuals of the same species. These variations are coupled with striking differences in the development of the head and mandibles and it is often possible to distinguish large (teleodont), small (priodont), and intermediate (mesodont) forms. In other cases there are no intermediates known between the extremes and species, like *Odontolabis sinensis*, consequently exhibit what has been termed high and low dimorphism. Lucanid larvæ inhabit the rotting wood of trees or their roots. They possess well developed antennæ and legs, the maxillæ are single-lobed and they differ from many Scarabæid larvæ in that the segments are not raised into three folds. The larva of *Lucanus cervus* stridulates by rubbing certain hard ridges on the third pair of legs over a rugose area at the base of the second pair: the third pair, however, is not specially modified or reduced in size as in the Passalidæ and *Geotrupes*. The duration of larval existence in this family does not appear to have been definitely ascertained: in *L. cervus* it lasts about four years, while certain other species are stated to require six years to complete their development. Pupation takes place in a cell formed of gnawed wood fragments. The holarctic genus *Sinodendron* is of an aberrant character and several recent authorities accord to it family rank. The species are completely cylindrical and instead of the mandibles differing in the male, the latter sex carries a cephalic horn. The thorax is very truncated in front and the antennæ are short and non-geniculate. The larva occurs in rotting wood of ash, etc.: it is more slender than the usual Lamellicorn type and gradually narrowed posteriorly. About 600 species of Lucanidæ are known but only three genera, each with a single species, occur in the British Isles.

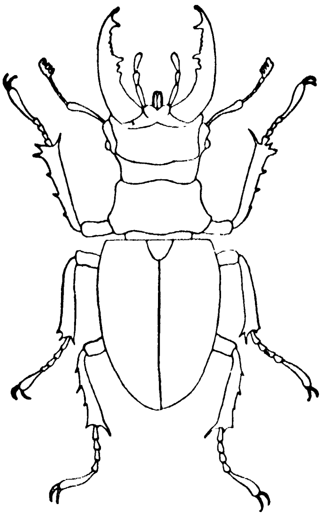

FIG. 518.—*Lucanus cervus*, Male, natural size. Europe.

FAM. SCARABÆIDÆ (Chafers, etc.).—A very large family of more or less convex insects, with the mandibles not specially developed in the males, and with the elytra not usually completely covering the abdomen. Over 14,000 species are known and about 90 occur in the British Isles. A classification of this extensive group, with a table of sub-families, is given by Arrow but only certain of the more important of the latter can be referred to here: a key to a number of the larvæ is provided by Perris.

The Cetoninæ are typically represented in England by the "rose chafer"—*Cetonia aurata*. They are exceedingly brilliantly coloured, mostly diurnal insects, especially found in the tropics, and number about 2,500 species. Their mouth-parts are adapted for dealing with soft or liquid food and the labrum is membranous and concealed; the mandibles, with few exceptions, are thin and incapable of biting, and the maxillæ are invested with long hairs. The larvæ are generally found among roots, in decaying wood, accumulations of dead leaves and other plant refuse. The life-histories of *Cetonia*, *Oxythyrea*, and *Protætia* have been followed by Fabre (*Souv. Ent.* 8). The larvæ of *P. cuprea*, and other species, inhabit the nests of *Formica* where they have been found consuming the woody material of which these habitations are composed. The Cremastochilini are exceptional in being mostly sombre-coloured nocturnal insects, living as larvæ and adults in the nests of ants and termites.

The Dynastinæ include some of the largest and most striking of all Coleoptera. The majority of this species are black and, being nocturnal or crepuscular in habits, they are not very often seen at large. They are chiefly remarkable on account of the extreme development of sexual dimorphism which is exemplified in the presence of large horny processes in the males. On the head there is usually a slender, recurved, and sometimes toothed or bifurcated frontal horn: on the prothorax there are commonly one or more processes which often arise from the margins of a dorsal cavity. In a few cases, e.g. *Oryctes rhinoceros* both sexes are horned. Many species possess stridulating organs consisting of a file-like area on the penultimate tergum which is rasped by the apices of the elytra. The Dynastinæ include about 100 species, almost all of which are tropical, and more especially neotropical. Very little is known of their biology, but their larvæ have been found in decaying vegetable matter, among roots, and in the stems of palms. Several species are injurious, their larvæ attacking the roots of sugarcane and rice. *O. rhinoceros* is a great pest of coco-nut plantations, its larvæ destroying the tissue at the leaf-bases and providing for the onset of decay.

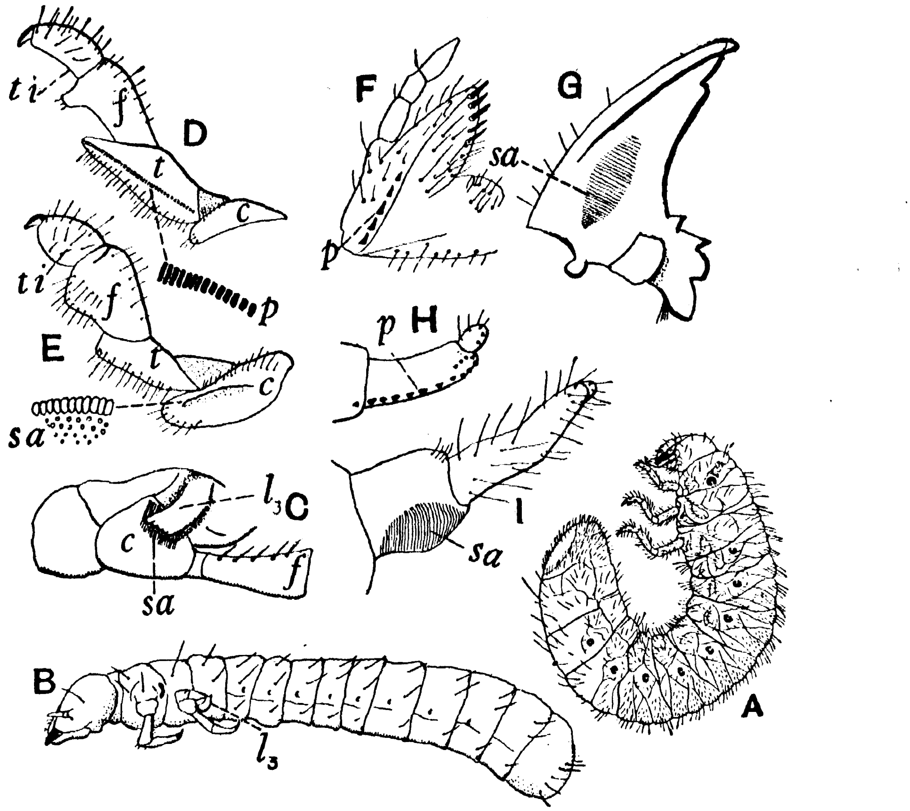

Fig. 519.—Lamellicorn Larvæ and Stridulatory Organs.

A, larva of *Anomala polita* (Scarabæidæ: *after* Gardner). B, larva of *Passalus* with C enlarged detail of part of 2nd leg and reduced 3rd leg. D, *Lucanus cervus*, 3rd leg and E, 2nd leg. F, *Phyllopertha horticola* left maxilla and G right mandible. H, *Geotrupes* 3rd leg and I, 2nd leg. *c*, coxa; *f*, femur; l_3, reduced 3rd leg; *p*, plectrum; *sa*, stridulatory area; *t*, trochanter; *ti*, tibia.

Banks (*Philippine Journ. Sci.* 1906) states that it will also develop freely in vegetable refuse and in soil. *O. nasicornis* is often found in decomposing bark refuse of tanneries in S. Europe.

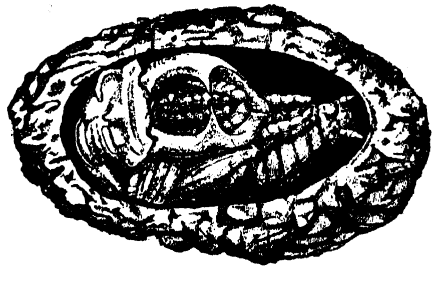

Fig. 520.—*Lucanus cervus*, Male Pupa in its Cell.

After Roesel.

The Melolonthinæ include the "cockchafers" and the common European *Melolontha vulgaris* (Fig. 517) formed the subject of the classical anatomical memoir by Straus-Durckheim. They differ from the two preceding groups in the presence of an evident chitinized labrum, and comprise nearly 4,500 species. The larvæ feed among decaying vegetable matter or among the roots of plants and are, in some cases, exceedingly injurious. In the case of *M. vulgaris* the eggs are laid in several batches of fifteen or more during early summer which are deposited to a depth of 6 to 8 inches in the ground. The larvæ hatch after an interval of about three weeks, and the insect remains in this stage for three years in England, and for a longer or shorter period in other countries according to climatic conditions. During the cold months the larvæ descend into the ground but, for the rest of the year, they come nearer the surface and devour the roots of corn, grass, etc., sometimes causing great injury. At the end of the third summer, they form oval pupal cells at a depth of two feet or more in the soil. The adults emerge about October but do not leave the ground until about the following May, when they are common about oak and other trees upon whose foliage they feed.

The Rutelinæ are likewise an extensive sub-family and many of the species are brightly coloured. In general facies they resemble the Melolonthinæ but are usually separable on account of the mobile claws which are of unequal size. They are represented in Britain by *Phyllopertha horticola,* whose imagines often devour the leaves and blossoms of roses and fruit trees, and *Anomala frischii.* Species of *Lachnosterna* are very destructive, as larvæ, in N. America.

The Geotrupinæ or " dor " beetles are large convex insects mostly of coprophilous habits. The labrum and mandibles are large and horizontal, the eyes are divided in front and the antennæ are 11-jointed. The best known species are those of *Geotrupes* of which *G. stercorarius* L. and its allies are familiar objects in Britain. They attract attention on still warm summer evenings by their blundering flight accompanied by a loud humming noise. The above species is evidently the " shard-borne beetle " of Shakespeare and the " drowsy beetle " of Gray's Elegy. *Geotrupes* constructs burrows about 18 inches deep in the earth, below a patch of dung, and portions of the latter are carried down to serve as food for the larvæ. Each burrow is filled at its blind end with a plug of dung in which a single egg is deposited. The larvæ stridulate very much after the manner of Passalids, only the hind-legs have suffered less reduction and the positions of the file and rasping organ are reversed. The adults stridulate by rubbing together a file on the hind coxæ and the sharp edge of the coxal cavity.

The Troginæ are a small group which differ from the Geotrupinæ in the labrum and mandibles being not horizontal. They mostly live in dried decomposing animal matter, and are represented in Britain by two species of *Trox.*

The Aphodiinæ are more or less oblong convex species of small size with concealed labrum and mandibles. They are useful scavengers and are found abundantly in dung. The extensive genus *Aphodius* is represented in Britain by about 40 species, and the larva of *A. fossor* is described and figured by Schiödte.

The Coprinæ are round or oval and often very convex beetles living almost entirely in dung. Their mandibles are membranous and incapable of biting. Much of our knowledge of their biology is due to Fabre, and the curious ball rolling habit of the sacred *Scarabæus* of the ancient Egyptians has attracted attention from very early times. Similar habits are met with among the close allies of this insect living in S. Europe, Asia and Africa. The ball is composed of dung which, in this form, is transported to a suitable retreat as food for the beetle itself. The mass of dung which contains the egg is pyriform and it is constructed in a separate underground chamber of material brought there for the purpose. In *Copris* this chamber is very large and is the combined work of the male and female. It contains two to seven pyriform cells of dung, each containing a single egg, and the " nest " is guarded and tended by the female. In some of the Indian species of *Heliocopris* and *Cartharsius* the egg balls are very large and coated with clay. When first discovered they were thought to be ancient stone cannon balls, and Lefroy mentions one being found 8 feet below ground. Certain species, including *Copris hispanus,* are unique among solitary insects in that the female, instead of dying after oviposition, tends her brood to maturity and then produces a second generation, but the number of eggs laid in each case does not appear to exceed four. Several genera are myrmecophilous and have the usual secretory glands and hair tufts indicative of symphiles. The sub-family is represented in Britain by *Copris lunaris* and several species of *Onthophagus.*

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Order 20. STREPSIPTERA ("Stylops")

SMALL, USUALLY ENDOPARASITIC, INSECTS; MALES WINGED AND FREE-LIVING, FEMALES MOSTLY LARVIFORM AND NEVER LEAVING THE HOSTS. MALE WITH CONSPICUOUS FLABELLATE ANTENNÆ AND DEGENERATE MOUTH-PARTS OF THE BITING TYPE. METATHORAX VERY GREATLY DEVELOPED: FORE-WINGS REDUCED TO SMALL CLUBBED HALTERES, HIND-WINGS LARGE AND FAN-SHAPED. FEMALE USUALLY APODOUS WITH HEAD AND THORAX FUSED: EYES AND ANTENNÆ ATROPHIED, MOUTH-PARTS VESTIGIAL OR WANTING. SEXUAL OPENINGS UNPAIRED AND SEGMENTALLY ARRANGED ON SEVERAL OF THE ABDOMINAL SOMITES. HYPERMETAMORPHOSIS PRESENT.

The order Strepsiptera comprises a small number of very anomalous insects whose larvæ exhibit an endoparasitic mode of existence which is retained throughout life in the female. In common parlance the adults are termed "stylops" and an insect harbouring these parasites is said to be "stylopized." Their hosts consist principally of members of the series Auchenorhyncha of the Homoptera and superfamilies Vespoidea, Sphecoidea and Apoidea among the Hymenoptera. Among the most extensively parasitized hosts are species of the Homopterous genus *Liburnia* and the genera *Vespa*, *Polistes*, *Halictus* and *Andrena* among Hymenoptera. The last-mentioned genus is more often attacked than any other and it includes a very long list of parasitized species.

The majority of English and American writers have included the Strepsiptera among the Coleoptera, placing them near the heteromerous families Meloidæ and Rhipiphoridæ, mainly on account of similarities in the larvæ and metamorphosis. The characters of the Strepsiptera, however, are so different from those of any other group of insects, that it appears desirable to regard them as an order of their own (vide Pierce 1909).

About 170 species are known and the majority have been discovered in the holarctic region, nevertheless, the order is also represented in the remaining zoo-geographical regions: a synopsis of British species of *Stylops* and *Halictoxenus* is given by Perkins (1918). All members of the order are very small or minute, the males commonly measuring about 1·5–4 mm. in length. In colour they are either black, or some shade of brown, and the portion of the female which protrudes from the host is usually yellowish brown.

External Anatomy (Fig. 521).—In the males the integument is very thin and in many parts transparent. The head is transverse, the compound eyes are very protuberant, and there are no ocelli. The antennæ are 4- to 7-jointed, but are variable in form and of peculiar structure: the third joint is flabellate, giving the antennæ a bifurcate appearance, and the succeeding joints may also be similarly produced, the antennæ then appearing as if branched. The surface of the joints is studded with complex sensory organs. The mouth-parts exhibit modification and great reduction from the normal biting type. Only vestiges of parts corresponding with the labrum and labium are recognizable; the mandibles are usually narrow and sickle-like or, more rarely, they are short and membranous, while a pair of 2- or 3-jointed organs have been variously interpreted as maxillæ or labial palpi. In the thorax the first two segments are greatly reduced, but the metathorax is very large, occupying at least half the length of the body. The legs are only used for clinging to the female during copulation:

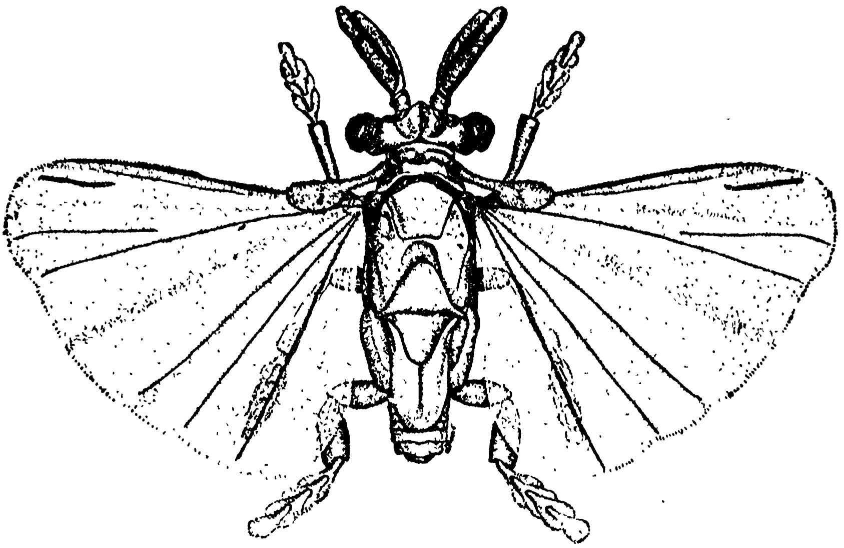

Fig. 521.—*Neostylops shannoni*, N. America: Male, Enlarged.
After Pierce, *Proc. U. S. Nat. Mus.* 54.

the tarsi are ordinarily 2- to 4-jointed, without claws, and usually each joint is provided with a ventral adhesive pad. The anterior wings are represented by small club-like processes, but the hind-wings are relatively large and fan-shaped, with radiating veins. The venation is degenerate; in the most generalized forms eight simple longitudinal veins are recognizable but their homologies in relation to the pupal wing-tracheation have not been determined, and there are no cross-veins. The abdomen is 10-segmented: an ædeagus or genital sheath encloses the penis and is located on the 9th sternum: cerci are absent.

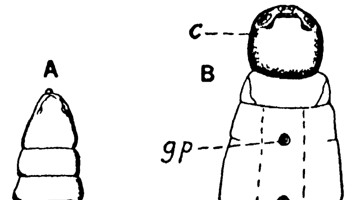

Fig. 522.—*Xenos vesparum*. A, Fully-grown Male Larva. B, Adult Female.
c, cephalothorax; *gp*, genital pores. Adapted from von Siebold.

The female (Fig. 522) is highly modified through degeneration in accordance with a permanently endoparasitic life. She is larviform, apodous, and enclosed in the persistent larval cuticle. The head and thorax are adnate forming a cephalothorax which is separated by a constriction from the long sac-like abdomen. Antennæ and eyes are wanting and the mouth-parts are vestigial: mandibles are present in some groups but wanting in others. The thorax is separated ventrally from the head by the aperture of the brood canal, which is a passage between the body of the female and the last larval cuticle, leading from the genital apertures to the exterior.

Internal Anatomy.—Our knowledge of the internal anatomy of Strepsiptera is mainly due to Nassonow whose work forms the basis of the account given by Pierce (1909). The alimentary canal is an unconvoluted tube of simple structure. In the male it exhibits three well-marked regions—the fore, middle and hind intestine, but there is no communication between the two latter parts of the gut: in the adult female the hind intestine has atrophied, the posterior end of the stomach being in contact with the integument of the last abdominal segment, there being no anal opening. The Malpighian tubes are only doubtfully represented by small papillæ. The nervous system is highly concentrated in both sexes: in the male the brain assumes much larger proportions than in the female, owing to the presence of the antennary and visual centres. The para-œsophageal connectives pass to a common ganglionic mass formed by the union of all the ventral ganglia up to, and including, the ganglia of the 2nd or 3rd abdominal segment: a median abdominal nerve cord terminates in a nervous centre formed by the coalescence of the posterior ganglia. The tracheal system opens to the exterior by one or two pairs of thoracic spiracles and, in the male, up to eight pairs of abdominal spiracles. The reproductive system is very similar in the larvæ of both sexes and consists of a pair of tubes lying one on either side of the gut. In the adult male, these organs maintain their paired structure, and communicate with the exterior by means of a common duct. In the female, the reproductive organs are stated to disintegrate, and the egg-masses are scattered through the body space. Cuticular invaginations, which develop into funnel-like tubes, function as genital ducts. The number of these apertures appears to vary from three to five: they are segmentally disposed on the median ventral region of the 2nd and following abdominal segments.

Biology and Host Relations.—The biology of these insects has been mainly studied with reference to species parasitizing Hymenoptera. The only tolerably complete study of the life-history of any species is the account given by Nassonow (in Russian) of *Xenos vesparum.* Male Strepsiptera are free-living, and usually only survive a few hours after emerging from their hosts. The females, on the other hand, remain permanently endoparasitic, and only the cephalothorax is visible externally, where it protrudes through the body wall of the wasp or bee. The males are by no means rare insects, but their small size and brief life cause them to elude the observation of most entomologists. They emerge from their hosts early in the morning, very soon after the latter have taken to the wing. Pairing takes place by the male alighting on the host, and inserting the ædeagus into the aperture of the brood canal of the female (Perkins): in some cases it appears probable that the eggs are able to develop parthenogenetically. The larvæ hatch within the body of the female and issue in large numbers (sometimes several thousand) through the genital canals previously alluded to. They pass into the space (or brood pouch) between the ventral surface of the parent and the persistent larval cuticle, ultimately emerging through the aperture of the brood canal. They then remain upon the body of the host until opportunity is afforded for escape. At this stage the young larvæ bear a resemblance to the triungulins of *Melöe*: they are very minute, active creatures with well formed eyes and legs, and pairs of long caudal setæ (Fig. 523). Their method of securing a new host has not been directly observed but, presumably, they leave the "maternal" hosts when the latter are on flowers, in the nest, or in other situations. If liberated on to flowers, they probably attach themselves to other host individuals that come along, and become transported thereby to the nests. Within the latter, they seek out the larvæ, and speedily burrow through the body-wall and become endoparasitic. Having entered the host, the stylopid larvæ undergo ecdysis, assuming an apodous maggot-like form in the second instar (Fig. 522). Their subsequent history has been followed by Nassonow in the case of *Xenos*. Nutrition appears to take place by the filtration of the host's blood through the delicate cuticle of the parasite. The parasite does not penetrate the organs of the host, but occupies the body space between them, pushing them out of position. At the 7th instar the parasitic larva works its way outwards, so as to protrude from the abdomen of the host and, at this stage, the wasp or bee has assumed the pupal condition. In the case of *Stylops* protrusion usually takes place through the intersegmental membrane between the 4th and 5th abdominal segments. The male parasite now undergoes pupation and the pupa is enclosed in the exuviæ of the two preceding instars. The rounded tuberculated apex of the puparium, thus formed, is the only region visible externally and the winged insect emerges by pushing open an operculum. The female parasite is recognizable by the flattened disc-like cephalothorax, the large white grub-like after-body remaining within the abdomen of the host.

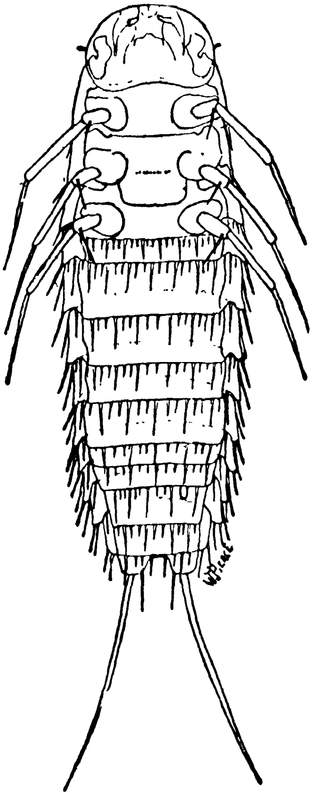

FIG. 523.—*STYLOPS CALIFORNICA*, TRIUNGULIN, VENTRAL VIEW, ENLARGED.

After Pierce, *loc. cit.*

Both sexes of the host are liable to parasitization but, in most cases, the largest number of attacked examples are females. As a rule, male parasites are the commoner, but both sexes may occur in the same individual host. The latter often nourishes several parasites: Pierce (1909) mentions the exceptional number of 31 larvæ in a single host and states that the largest number of male puparia found exserted from the body of a host is 15. The effects of stylopization on the hosts have been studied by Pérez (1886), Smith and Hamm (1914), Perkins (1918) and others with reference to *Andrena* and by Salt (1931) in *Vespids*; the whole subject is also discussed by Pierce and by Wheeler. In the first-mentioned genus, stylopized examples often exhibit a shorter and more globular abdomen with increased pilosity, the head is usually smaller than in normal specimens, while the puncturation of the body becomes finer, but different individuals do not necessarily react similarly to the presence of the parasite. These changes are common to both sexes and affect the specific characters. Much confusion has consequently arisen through the founding of new species on stylopized individuals. The following changes affect the secondary sexual characters. (1) Parasitized females have the pollen-collecting apparatus so diminished that the hind-legs resemble those of the males. (2) The clypeus or frons in the males is normally marked with a greater amount of yellow than in the females: stylopization may result in the females acquiring the yellow coloration of the males, and individuals of the latter sex having the light colour very markedly diminished. (3) The sting is curtailed in size and the copulatory apparatus of the male suffers reduction. Certain minor changes may also occur and Pérez concludes that, in the case of *Andrena*, secondary sexual modifications induced by stylopization are inversions of development, and that parasitized examples are not merely diminished individuals, but that the female acquires certain characters belonging to the male and the male develops certain of those which pertain to the female.

Before maturity the parasites live on the fat-body and blood-tissues of the hosts. As already mentioned, they do not directly attack the other organs but the latter undergo partial atrophy through inadequate nutrition. The gonads become more or less reduced in size, and the oocytes degenerate in their follicles. There is no evidence that the females are ever fertile, but the males are known to be capable of producing spermatozoa, and parasitized examples of both sexes of *Andrena* have been taken *in copula*.

Much less information is available with regard to the stylopization of Homoptera. The phenomenon is known among the Jassidæ, and various members of the Fulgoroidea: according to Perkins (1905) either nymphal or adult hosts may produce mature parasites, which protrude through the tergal, sternal, or pleural regions of the abdomen. *Elenchus* is a parasite of the Fulgorid genus *Liburnia* in England.

Hitherto, there has been every reason to regard Strepsiptera as being exclusively parasites. Exceptions to this generalization have recently come to light from the researches of Parker (1933) and of Silvestri (1933) with reference to the genera *Eoxenos* and *Mengenilla* respectively, both of which occur in Southern Europe. The females show no adaptation to parasitic life and are only known in the free-living condition, unassociated with any host. The head and thorax are distinct, without trace of the usual intimate fusion, while the antennæ, legs and eyes are present in a functional condition. The males show typical Strepsipterous characters and the larvæ are triungulins which show evident differences in the two sexes. In *Mengenilla* both sexes pass through a pupal instar. Little is known of the biology of these remarkable forms; in *Eoxenos* the various phases have been found beneath stones.

Classification.—The Strepsiptera are divisible into six principal families and a general account of the order, with a full bibliography, is given by Ulrich (1927). About sixteen species are known from Great Britain.

1 (4).—Tarsi of male 5-jointed with paired claws.
2 (3).—Antennæ of male 7-jointed with 3rd and 4th joints produced into flabellate lobes; female unknown. *Mengea*, *Triozocera*. MENGEIDÆ
3 (2).—Antennæ of male 6-jointed with 3rd to 5th joints produced into flabellate lobes: female free-living. *Eoxenos*, *Mengenilla*. MENGENILLIDÆ
4 (1).—Male with 4 tarsal joints or fewer and no claws.
5.—Female with 12 or more genital tubes: male unknown. *Stichotrema*. STICHOTREMATIDÆ
6.—Tarsi of male 4-jointed: 4 or 5 genital tubes. *Stylops*, *Xenos*. XENIIDÆ
7.—Tarsi of male 3-jointed: female with 2 genital tubes. *Halictophagus*, *Pentozocera*. HALICTOPHAGIDÆ
8.—Tarsi of male 2-jointed: female with 3 genital tubes. *Elenchus*. ELENCHIDÆ

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Order 21. **HYMENOPTERA** (Ants, Bees, Wasps, Ichneumon Flies, etc.)

INSECTS WITH TWO PAIRS OF MEMBRANOUS WINGS, OFTEN WITH THE VENATION GREATLY REDUCED, OR ALMOST ABSENT; THE HIND-WINGS SMALLER THAN THE FORE PAIR AND INTERLOCKED WITH THE LATTER BY MEANS OF CHITINOUS HOOKLETS. MOUTH-PARTS PRIMARILY ADAPTED FOR BITING AND OFTEN FOR LAPPING OR SUCKING ALSO. THE ABDOMEN USUALLY BASALLY CONSTRICTED AND ITS FIRST SEGMENT FUSED WITH THE METATHORAX; AN OVIPOSITOR ALWAYS PRESENT AND MODIFIED FOR SAWING, PIERCING, OR STINGING. METAMORPHOSIS COMPLETE; LARVA GENERALLY APODOUS WITH A MORE OR LESS WELL DEVELOPED HEAD, MORE RARELY ERUCIFORM WITH LOCOMOTORY APPENDAGES; TRACHEAL SYSTEM PERIPNEUSTIC THROUGHOUT LIFE, OR AT LEAST IN THE FINAL INSTAR. PUPÆ EXARATE AND A COCOON GENERALLY PRESENT.

This order is one of enormous extent comprising probably about 60,000 described species and many thousands of forms still await discovery. If the Hymenoptera be judged by their intelligence, as betrayed by their actions, they must be regarded as including the highest members of their class. Structurally the majority of their species have attained an advanced degree of specialization which is only surpassed by the Diptera. In certain species of the order the individuals have acquired the habit of living together in great societies, as in the case of the ants, wasps of the family Vespidæ and bees of the families Bombidæ and Apidæ. A large proportion of the members of these societies have undergone structural changes, in some cases slight, in others more pronounced, so that they constitute a separate caste or type of individual known as the worker. These worker forms are imperfect females whose power of reproduction is either in abeyance or usually limited to the laying of male-producing eggs. Their functions include those of nest-building, feeding and tending the brood and the defence of the colony. The normal reproduction of the species in the social Hymenoptera is either performed, as in certain wasps, by all the female members of a colony or more usually by a single individual of large size known as the queen. The sole function of the males is that of impregnating the females, an act which often comparatively few succeed in consummating.

Indications of what, in the higher Hymenoptera, constitutes social behaviour are found among solitary wasps and bees (vide Wheeler, 1928). Thus, Verhoeff observed that the female *Halictus quadricinctus* constructs a number of cells associated with a common entrance tunnel in the ground. These cells resemble a rude comb and, after being provisioned and closed, are guarded by the parent who may even survive until the adults emerge. Solitary bees and wasps practise "mass provisioning"—i.e. they store their cells with sufficient food to satisfy their developing offspring and close them down before the eggs hatch. There are, however, species which feed their larvæ from time to time ("progressive provisioning"), thus becoming acquainted with their offspring. Among tropical Vespidæ of the sub-families Ropalidiinæ and Epiponinæ primitive types of social life are evident. They live in perennial colonies, containing numerous fecundated females, and their offspring are reared by progressive provisioning. Workers are either absent, or but slightly differentiated, and numerically weak. Such colonies, when fully developed, often emit swarms consisting of fecundated females – sometimes accompanied by workers. This polygynous state is possibly more primitive than what obtains among the Vespidæ of temperate zones, whose colonies are monogynous and dominated by a single fecundated female or queen: such colonies are seasonal only and the worker caste is clearly differentiated. The Bombidæ are the most primitive among social bees. They construct no true comb, their cells resembling those of solitary bees: their young are fed at first by mass provisioning, but the cells are opened later periodically to feed the older larvæ. In temperate regions their colonies are monogynous and only last for a season. Among the Apidæ the colonies are perennial and monogynous, giving off swarms. *Melipona* and *Trigona* practise mass provisioning and close their cells: they are, in fact, the only social Hymenoptera where there is complete absence of contact between parent and brood; in many cases the three castes are all reared in identical cells on a similar diet. In *Apis* the cells are open throughout larval development: the castes are reared in differentiated cells and queen-producing larvæ are fed on a specialized diet. Among ants the castes exhibit their maximum differentiation: the larvæ are reared in clusters, there being no cells, and there is a more intimate acquaintance between the workers and the brood than in other social Hymenoptera.

The phenomenon termed by Wheeler *trophallaxis*, or the mutual exchange of food between imagines and their larvæ, is of general significance among those social Hymenoptera which adopt progressive provisioning. Among the Vespidæ the larvæ, either before or after feeding, exude saliva which is eagerly imbibed by the attendant imagines. Ant larvæ also produce secretion highly acceptable to their nurses. In some species it is saliva, in others an exudation of the integument, while in the Pseudomyrminæ it is a product of special papillæ or appendages known as exudatoria. It appears that an avidity for these larval secretions, rather than maternal solicitude, initiates and sustains the bond between social Hymenoptera and their brood. Trophallaxis is also evident among termites: and it further accounts for the relations which both ants and termites have acquired with alien insects and other arthropods (vide Wheeler 1923). Among bees the phenomenon seems wanting: possibly the storing of pollen and honey, which can readily be obtained, has rendered the exploitation of larval secretions unnecessary.

Hymenoptera are also remarkable on account of the highly evolved condition which parasitism has reached in the order, and it has been independently acquired among species belonging to very diverse superfamilies The Symphyta are essentially phytophagous, nevertheless *Oryssus* is parasitic in its larval stage, but its habits have been very little studied. Among the Apocrita, about one half the known species of Cynipoidea are parasites, and this same habit occurs in the whole of the Ichneumonoidea and Proctotrypoidea, and in almost all the Chalcidoidea. Associated with parasitism is the phenomenon of polyembryony (vide p. 164) which is known to occur in a few of the Chalcidoidea and Proctotrypoidea. Among the aculeate families true parasitism is much rarer and, in the majority of cases of this kind, their larvæ devour the provisions accumulated by the host for its own progeny. This involves the destruction of the latter but it is not parasitism in the strict sense. For a general discussion of parasitism in its different phases, and the more important literature thereon, reference should be made to papers by Wheeler (1919) and Brues (1921).

The effects of hymenopterous parasites upon their hosts vary in different cases. Certain of the Chalcid parasites of Coccidæ are bivoltine. One generation attacks the young hosts who fail to reach maturity and succumb to the parasitism. The following generation of parasites attacks the older hosts and, in this case, the females of the latter are usually able to lay some or even all their ova prior to being overcome by the parasites. Wheeler has shown that the ectoparasite *Orasema* produces abortion, or malformation, of certain parts in the ants which it attacks, and none of the latter become imagines. Certain of the Dryinidæ are known to parasitize nymphal Homoptera and may modify or otherwise inhibit the development of the secondary sexual characters of their hosts. Lists of parasites and their hosts are given in the catalogues of Dalla Torre (1892–02), de Gaulle (1898) and of Leonardi and Boselli (1922, 1928). In so far as the hosts are British species, the papers of Morley on the parasites of Coccidæ (*Entom.* 42 and 43) and other Hemiptera (*Zoologist,* 1909) are useful, also the papers by Elliott and Morley (*Trans. Ent. Soc.* 1907, 1911) on those of the Coleoptera.

Parthenogenesis (vide also p. 163) is more frequent among Hymenoptera than in any other order of the animal kingdom, and this method of reproduction is prevalent in a number of widely separated families. In many it is not an occasional phenomenon, but plays an important part in the continuity of the species, and may also be accompanied by an alternation of generations. The best known instance of parthenogenesis is found in the honey bee, in which unfertilized eggs, whether laid by the queens or by fertile workers, produce males and the same applies to *Vespa.* Among ants parthenogenesis has been less thoroughly investigated, and it has been claimed that the unfertilized eggs similarly only give rise to males, but Reichenbach, Donisthorpe and others have shown that the workers are capable of laying unfertilized eggs which develop into other workers. In the Cynipidæ both sexes may be produced parthenogenetically and the generations, which arise in this way, alternate with those produced by the sexual method. In other species heterogeny is absent, and females are produced parthenogenetically generation after generation ; in some cases males are absent and in others rare. Among the Tenthredinidæ parthenogenesis is also prevalent ; in certain species only males arise from the unfertilized eggs, in others only females, or both males and females may be produced. In some Chalcidoidea parthenogenesis is the usual method of reproduction as in *Aphelinus mytilaspidis* and *Harmolita grandis,* in which examples males are very rare. Many other parasitic Hymenoptera are capable of both sexual and parthenogenetic reproduction and, in these cases, the latter process generally gives rise to males.

General Structure of the Imago

The general structure of the Hymenoptera has been well investigated in comparatively few types. The work of Snodgrass (1925) on the anatomy of the honey bee will serve as an introduction to the general morphology of the order. For the Formicoidea the numerous papers by Janet should be consulted: for the Ichneumonoidea Seurat's study (1899) of *Doryctes* is important, and for the Chalcidoidea Grandi (1929) has investigated th structure of *Blastophaga* with great completeness.

A. EXTERNAL ANATOMY

THE HEAD is free from the thorax and often extremely mobile. It varies considerably in form and, as a rule, the long axis is the longitudinal one. The cranial capsule is very completely consolidated but both clypeus and labrum are usually distinct; the epipharynx is well developed and trilobed in the higher forms, the median lobe being pointed and projecting. Acuteness of vision is a characteristic of the order and the compound eyes are therefore almost always large; in the male they are sometimes strongly convergent or holoptic. In certain species of ants belonging to the genera *Dorylus* and *Eciton* the eyes have atrophied, and in other species of the latter genus, they are reduced to a single facet on either side. Three *ocelli* are commonly present but, in some cases, they are aborted, as in the Bembecidæ and in the workers of many of the ants. The *antennæ* are extremely variable in character in the Symphyta and among the parasitic families of the Apocrita. As a rule, they are longer in the males than in the females, and frequently exhibit pronounced sexual dimorphism. The latter feature attains its greatest development among the Protoctrypoidea and Chalcidoidea, where these organs in the male may be either filiform, clavate, pectinate, branched or verticillate. The number of joints present is singularly inconstant in the lower superfamilies: thus among the Ichneumonidæ, for example, it may be as low as 14, or as high as 70. In the sawfly *Hylotoma* there are only three joints, and four are present in some of the ants. In the Sphecoidea, Vespoidea and Apoidea the number for the most part is fixed, there being usually 13 joints in the males and 12 in the females.

THE MOUTH-PARTS exhibit a wide range of differentiation from the generalized biting, orthopterous type found among the Symphyta to the highly modified sucking type of *Apis*, *Euglossa* and other bees. Mandibles are universally present throughout the order but, except in the predaceous members of the Tenthredinidæ, their principal function is industrial rather than trophic. They are used to enable the imagines to cut their way through the walls of their hosts in the case of the parasitic superfamilies, while among the Sphecoidea, Vespoidea and Apoidea their principal functions are the gathering of material and nest-building. If the mouth-parts of *Nematus*, or other typical sawfly (Fig. 524), be examined it will be observed that well-developed dentate mandibles are present; the complete number of parts are evident in the maxillæ, and their palpi are 6-jointed. In the labium both mentum and submentum are well developed, the labial palpi are 4-jointed, and the ligula appears deeply cleft into three nearly equal lobes—a median glossa and lateral paraglossæ. Among the Apocrita this same type of mouth-parts is retained in the parasitic groups, but it has undergone a variable amount of specialization. The labial and maxillary palpi usually exhibit a reduction in the number of their joints, particularly in the Chalcidoidea. The maxillæ are frequently single-lobed, and the ligula is commonly formed by the broadened glossa, the paraglossæ being either vestigial or absent. In the higher superfamilies, the glossa becomes increasingly prominent, in conformity with the habit of feeding upon and collecting nectar. This organ becomes progressively lengthened, the associated mouth-parts become attenuated accordingly, and the result of these modifications is the formation of a proboscis. The latter organ is an adaptation which is necessary in order to extract the juices from the deeply seated nectaries of many flowers.

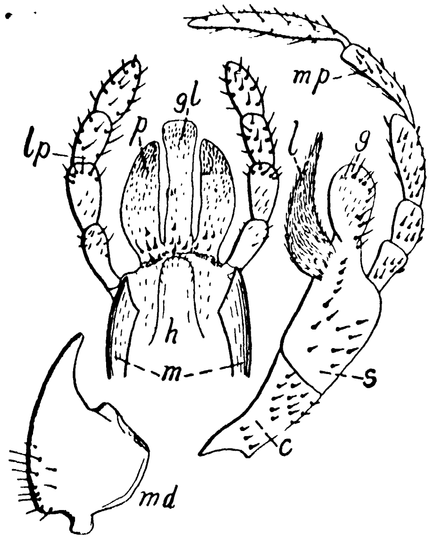

FIG. 524.—MOUTH-PARTS OF A SAW-FLY.
h, hypopharynx; other lettering as in Fig 525

It is possible to trace the evolution of the proboscis in different genera of the Apoidea, from the simple condition found in the Colletidæ and Prosopidæ, up to the highly specialized apparatus seen in *Apis*, *Euglossa*, etc. In the two previously mentioned families the glossa is extremely short and broad with a bifid extremity; the labial palpi are non-sheathing and 4-jointed, and the maxillary palpi are 6-jointed. In *Andrena* the glossa, although still short, is acuminate, while in *Panurgus* and *Nomada* it is appreciably lengthened, as are also the labial palpi and the maxillary lobes. In *Melecta* the first two joints of the labial palpi ensheath the greatly drawn out glossa, and the maxillary palpi are reduced to small 4-jointed organs. In *Psithyrus* and *Bombus* the glossa is still further elongated, and the maxillary palpi are represented by inconspicuous 2-jointed organs, while in *Apis* they have undergone further degeneration and are in the form of minute single-jointed papillæ. In *Anthophora* the glossa is longer than in any other British bees, but the two pairs of palpi are not specialized to a correspondingly high degree. In the tropical *Euglossa* the maxillary palpi are single jointed, the labial palpi 2-jointed and the glossa attains a length exceeding that of the whole insect.

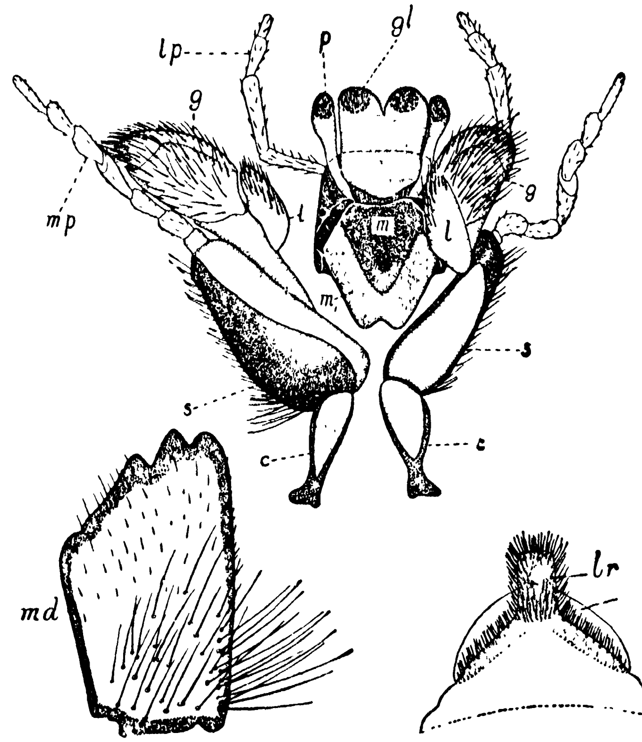

FIG. 525.—MOUTH-PARTS OF *VESPA GERMANICA* (WORKER). ONE MAXILLA IS SHOWN EXTENDED AND THE OTHER IN ITS NATURAL POSITION.

c, cardo; *e*, epipharynx; *g*, galea; *gl*, glossa; *l*, lacinia; *lp*, labial palp; *lr*, labrum; *m*, mentum; m_1, submentum; *md*, mandible; *mp*, maxillary palp; *p*, paraglossa; *s*, stipes.

In Figs. 524, 525 and 526 the mouth-parts of a saw-fly, *Vespa* and *Apis* are represented. In the case of the first mentioned type the essentially biting nature of their component parts is evident. In *Vespa* these organs are adapted both for biting (and mastication) and licking. The maxillæ are comparatively little modified; the cardines and stipites are well developed, and the palpi are 6-jointed. The laciniæ are reduced to small scales, while the galæ assume the form of broad 2-jointed membranous lobes. The labium is composed of a large shield-shaped mentum, the ligula is represented by the curious elongated paraglossæ and a wide bilobed glossa, while the palpi are slender 4-jointed organs. In *Apis* the mouth-parts are highly modified to form a proboscis and the glossa has become a sucking organ. The chief basal plate or stipes of the maxilla represents, morphologically, the combined stipes and palpifer: at its proximal end the stipes is articulated with the stalk-like cardo, and near its apex on the outer border, is a minute peg-like maxillary palp. Articulating with the distal extremity of the stipes is a large blade-like lobe or galea; a reduced lacinia is present though often overlooked. In the labium, the large strongly chitinized basal plate is the mentum, and the latter articulates distally with a small triangular sclerite or submentum. The base of the latter is supported by a flexible transverse band the *lorum* (lora of some authors) whose extremities are attached to the distal ends of the cardines. The labial palpi are conspicuous 4-jointed organs, each being carried by a basal palpiger. The elongate central organ of the proboscis is the glossa (often erroneously termed the hypopharynx, lingua or ligula), and at the base of the latter are two small concealed lobes or paraglossæ. The glossa is invested with long hairs and at its apex is a small spoon-shaped lobe—the *labellum* or bouton. The side walls of the glossa are inclined downwards and inwards, until they almost meet along the mid-ventral line, and thereby form the boundaries of a central cavity. Embedded in the roof of the latter is a longitudinal rod which is grooved along its entire length, and this groove is converted into an imperfect tube by means of two rows of hairs which converge from its margins. The dorsal rod is flexible and becomes continuous basally with the ventral supporting plate of the ligula. The lining of the cavity of the glossa and its rod can be evaginated through the cleft, a process which admits of the cleansing of the parts in question. In transverse sections, the space between the outer and inner walls of the glossa is seen to contain blood and is in communication with the head cavity. The complete extension of the organ is due to blood pressure. Its retraction is partly due to the release of that pressure, and partly to the contraction of muscles inserted into the base of the dorsal rod. The latter, when drawn backwards, shortens the glossa which, as Snodgrass remarks, become bushy just as does a squirrel's

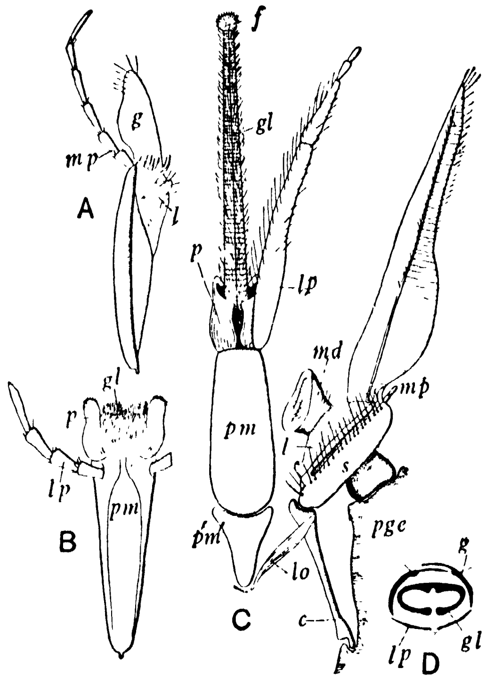

FIG. 526.—MOUTH-PARTS OF BEES.

A, *Prosopis*, right maxilla and B, labium (ventral) *Apis*. C, mouth-parts (ventral) D, cross section of same when feeding, *f*, flabellum, *lo*, lorum; *pge*, postgena; *pm*, prementum; *p'm'*, postmentum. Other lettering as in Fig. 5 .5.

tail if one attempts to pull out the bone at the base. When at rest, the mouth-parts are folded down beneath the head against the stipites and mentum. During feeding they are straightened out with the two modified proximal joints of the labial palpi closely applied to the glossa, and partly embraced by the ensheathing laciniæ. The glossa is very active while food is being imbibed : not only is the whole ligula alternately retracted into and protruded from the base of the mentum, but the glossa itself alters its length in the manner just described. The liquid food ascends by means of capillary action in the central channel of the glossa, and the effect of the shortening of the latter organ is to squeeze the nectar backwards, until it enters the space between the paraglossæ, and so on into the mouth. Its passage onwards is probably ensured by means of a sucking action exerted by the pharynx. For a detailed investigation of the structure and mode of action of the proboscis, and its musculature, reference should be made to the memoir by Wolff (*Nova Acta Ksl., Leop.-Carol. Akad.*, 66, 1875) and to that of Snodgrass (1925) : the anatomy of this organ in different genera of bees is described by Saunders (1890) and Demoll (1908).

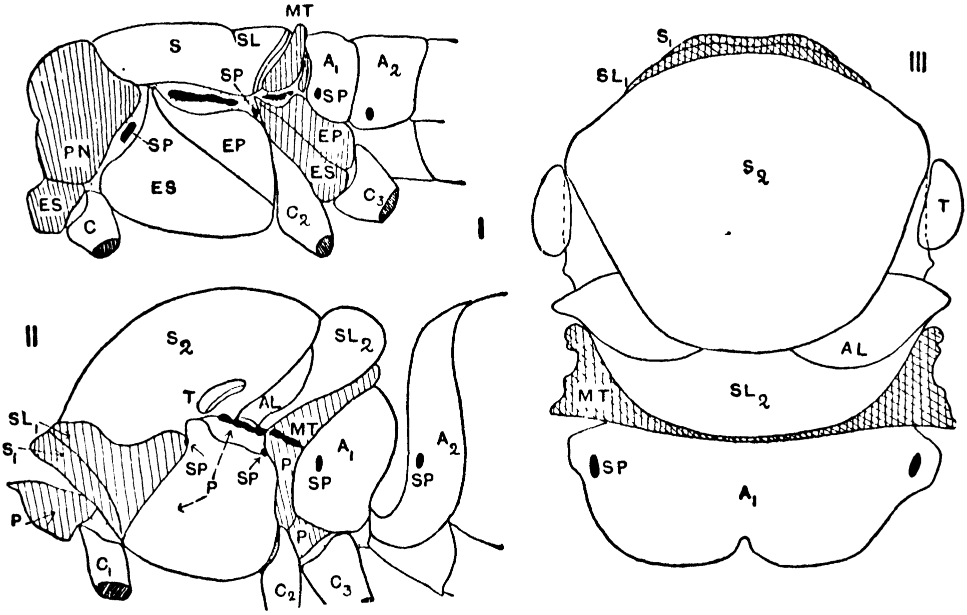

FIG. 527.—I, *Sirex*, LATERAL ASPECT OF THORAX. II, *Apis mellifica*, LATERAL ASPECT OF THORAX. III, DORSAL ASPECT OF SAME.

A_1, A_2, 1st and 2nd abdominal segments ; *AL*, axilla ; *C*, coxa ; *EP*, epimeron ; *ES*, episternum ; *MT*, metanotum ; *P*, pleuron ; *PN*, pronotum ; *S*, scutum ; *SL*, scutellum ; *SP*, spiracle ; *T*, tegula. (Pro- and meta-thorax are lined, mesothorax and abdomen are left plain)

THE THORAX of Hymenoptera (Fig. 527) is principally characterized by the fusion of the first abdominal segment with the metathorax, and its complete incorporation in the latter region—a change which is brought about during the prepupa. The transferred abdominal segment is termed the *propodeum* which was first described by Latrielle as the "median segment." Among the Symphyta the latter is still evidently part of the abdomen and has undergone but little specialization. In the Apocrita it has become transferred to the thorax and fused up with the metapostnotum and metapleura. Its existence in all cases, however, may be ascertained by the fact that it bears the first pair of abdominal spiracles. The study of the thorax in the order, as a whole, indicates that a progressive series of modifications has taken place in the higher forms (vide Snodgrass, 1910).

The *pronotum* is dismembered from the body of the prothorax and attached to the front of the mesothorax. The sternum and pleura are fused to form the *propectus*, which supports the head and carries the anterior pair of legs. The *mesonotum* is completely divided by a membranous transverse suture into an anterior plate or *scutoprescutum*, and a posterior plate or *scutellum*. In the Chalcidoidea (Fig. 528), and other of the parasitic forms, the sides of the mesoscutum are separately demarcated as *parapsides*, and similarly the lateral walls of the mesoscutellum may be separately developed to form sclerites which are often termed *axillæ*. Tegulæ are very generally present throughout the order. The *meso-postnotum* and its phragma are concealed through being invaginated within the cavity of the thorax: the phragma is often extensive, and may extend backwards into the base of the abdomen as in *Aphelinus* and other Chalcids. The *metanotum* is reduced to a single transverse plate carrying the hind-wings, while the *metapostnotum*, in all the higher members of the order, is indistinguishably merged into the front margin of the propodeum.

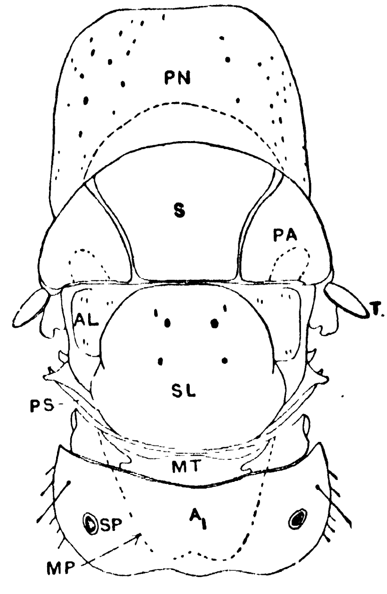

FIG. 528.—DORSAL ASPECT OF THE THORAX OF A CHALCID (*PHILOTRYPESIS CARICÆ*).

MP, mesophragma; *PA*, parapsides; *PS*, postscutellum of mesothorax. Other lettering as in Fig. 527. *After* Grandi, *Boll. Lab. Zool. Portici*, 14, 1921.

THE WINGS. No insects have deviated so far from the primitive venational type as the Hymenoptera, and even the most generalized members of the order are highly specialized as regards the wing veins. Great difficulties confront any attempt to determine their homologies and, as Comstock has pointed out, the courses of the tracheæ do not afford a reliable clue in this respect. An examination of the young pupæ of the honey bee also reveals the fact that the venation is already foreshadowed before the tracheæ develop, and that the latter are formed after the vein cavities are laid down. We have, therefore, to depend very largely upon comparative studies within the order and also with members of related orders. A dominant feature is the extensive fusion of the principal veins and the tendency of their branches to assume a transverse course, and also to become coalesced from the wing-margin inwards. This venational specialization in Hymenoptera renders the Comstock-Needham system of nomenclature very difficult to interpret, in many cases, by the general student. It has, therefore, been deemed desirable to offer an alternative terminology (that largely used by Cresson: Figs. 531, 532) which also affords greater facilities for reference and has been adopted in the keys to the families. Owing to multiplicity of systems that have been brought forward, and the want of agreement in the terminology used, reference should be made to a paper by Rohwer and Gahan (1916) which provides a key to the greatly involved synonymy of vein- and cell-nomenclature. In so far as the Symphyta are concerned, the venation has received a good deal of attention from MacGillivray (1906) but the Apocrita have not been studied with similar thoroughness. In the saw-fly *Pamphilius* and in *Siricidæ* (Figs. 529, 530) the venation is more generalized than in most other members of the order but, even in these cases, the principal veins have undergone extensive coalescence and the branches of the forked veins are greatly modified. Specialization by reduction and fusion is evident throughout the Apocrita.

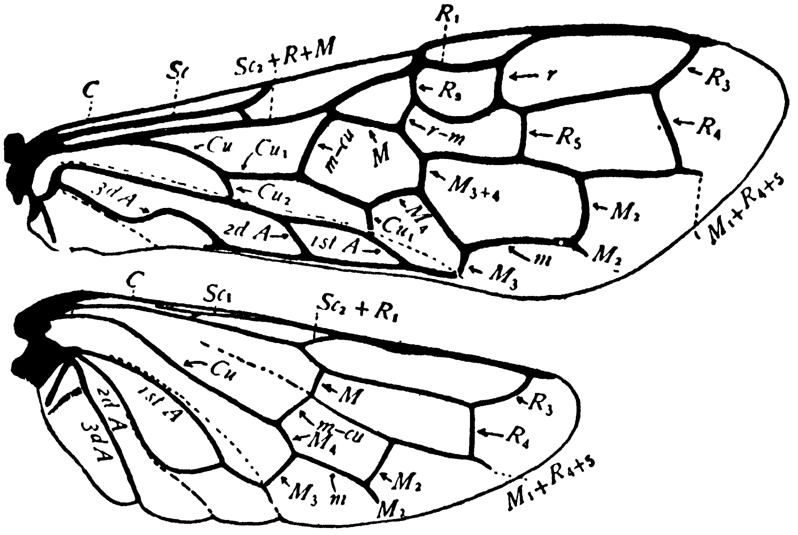

FIG. 529.—RIGHT WINGS OF A SAWFLY (*PAMPHILIUS*) WITH THE VEINS LETTERED. *After* Comstock "Wings of Insects."

These features attain their maximum development among certain of the Evaniidæ and in the Chalcidoidea, where there is a solitary compound vein, running near the costa of the fore-wing, and the hind-wing is veinless; in the Platygasteridæ both pairs of wings are devoid of veins. Throughout the order the wings of each side are held together by a row of hooks or *hamuli* along the costal margins of the hind pair: these hooks catch on to

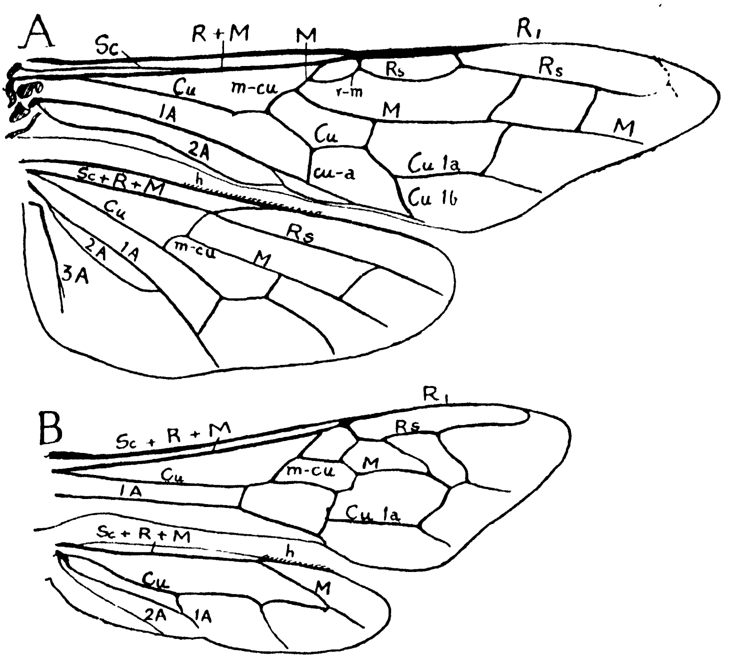

FIG. 530.—A. RIGHT WINGS OF *SIREX GIGAS* AND B. *APIS MELLIFICA*. *h*, HAMULI.

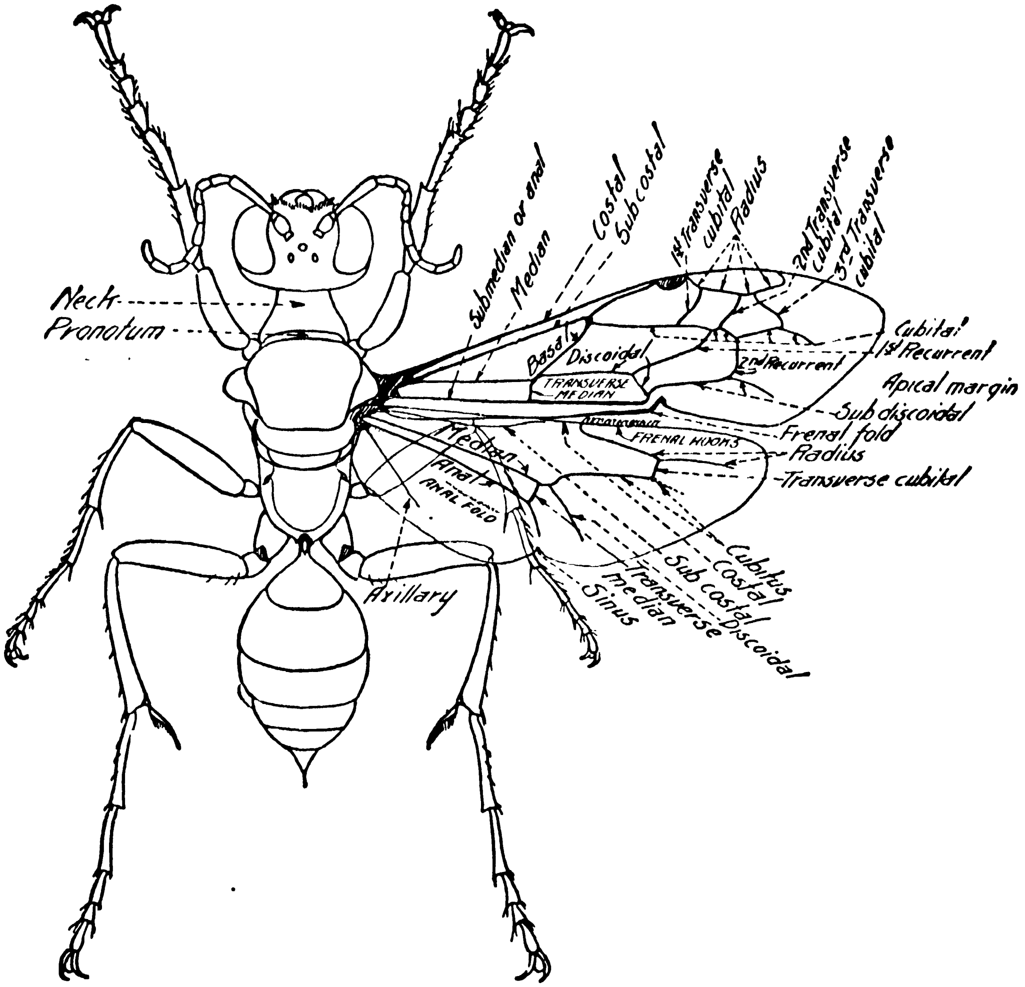

FIG. 531.—*Chlorion* (*Ammobia*), TYPICAL SPHECOID, WITH THE OLDER NOMENCLATURE OF THE WING-VEINS.

After Rohwer, *Bull.* 22, *Connecticut Geol. and Nat. Hist. Survey.*

a fold along the posterior margin of the fore-wing, so that the wings of a side become interlocked. Among the Chalcids the hamuli are reduced to a localized group of two or three hooks and, in the Mymaridæ, the latter may be totally wanting. Apterous forms are a common feature in the order, and are the rule among the workers of all species of ants, and occasionally also among the males of these insects and of many Torymidæ. Wingless females are present in the Mutillidæ, Thynnidæ and Myrmosidæ, in which families the males alone are winged. Similarly apterous females occur frequently in the

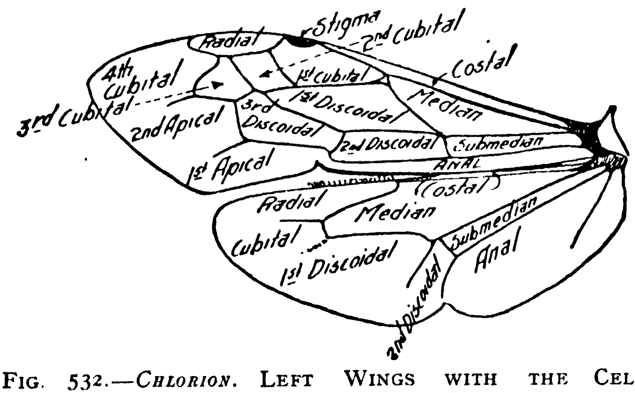

FIG. 532.—*Chlorion.* LEFT WINGS WITH THE CELLS NAMED ACCORDING TO THE OLDER NOMENCLATURE.

After Rohwer, *loc. cit.*

Proctotrypoidea and in certain of the Ichneumonidæ and Braconidæ. Apterous members of both sexes of the same species are rare but are known, for example, in the Diapriid *Platymischus*, and in certain members of the Ichneumonid sub-family Cryptinæ.

THE LEGS exhibit various modifications: in all the parasitic groups, excepting the Pelecinidæ, the trochanters are commonly 2-jointed. In many forms, the spur or calcar at the apex of the fore-tibia is knife-like in character, and fits against a semicircular emargination of the basal joint of the tarsus. This cavity is beset with fine comb-like teeth, and the antennæ are repeatedly passed through the apparatus, which functions as a preening organ. The Sphecoidea, and the majority of the Vespoidea, are often termed the " Fossores," and their legs are adapted for digging and running, or for nest-building. In the Apoidea, the legs are comparatively simple in certain primitive genera but, in the higher forms, the posterior pair is adapted for pollen-carrying. The posterior tibia is more or less dilated and margined with long hairs, being thus modified to form a *corbicula* or pollen basket. The metatarsus is flattened on its inner aspect, and provided with several rows of short stiff spines which form a brush or *scopa*; by means of the latter the bee gathers the pollen adhering to the hairs of its body. When a sufficient quantity has accumulated on the brushes, it is scraped off over the edge of the hind-tibia of the opposite side and stored in the pollen basket. As a rule the tarsi of Hymenoptera are 5-jointed, and an empodium is present between the claws.

THE ABDOMEN is restricted physiologically to the region which commences with the second segment, the first abdominal segment being the propodeum already referred to. The number of segments that can be identified in the imago varies very greatly: the maximum number of nine can be distinguished in the Tenthredinidæ, while among the Chrysididæ it is difficult to make out more than four. As a rule, in the higher groups, there are six exposed segments in the females and seven or eight in the males. In the Symphyta the first abdominal (second actual) segment is always unmodified and forms a broad base of attachment. In the Apocrita this region is wholly or partially constricted to form a narrow neck-like zone, which is termed the *petiole* or *pedicel*. In the honey bee the latter is so short as to be only visible when the abdomen is deflexed. Almost every transition can be found between this condition and the extremely attenuated bristle-like petiole of *Sphex*, *Sceliphron* and other genera.

THE OVIPOSITOR (Fig. 533) is a very highly developed organ which is modified in different groups for sawing, boring, piercing or stinging but, in all cases, it exhibits a fundamental similarity of structure. Its general anatomical features are well exhibited in the hive bee and have been fully investigated by Kraepelin, Cheshire, Snodgrass and others. Morphologically, the ovipositor is composed of three pairs of gonapophyses, which have been shown by Zander to arise from a similar number of abdominal processes in the larva – one pair on the eighth segment and two pairs on the ninth segment. Those belonging to the first pair develop into the stylets, the middle pair on the ninth segment fuse to form the stylet-sheath, and the outer pair give rise to the palp-like processes. The actual sting or *terebra* is a hollow organ formed of three pieces bounding a central canal. The dorsal part or *stylet-sheath* has three functions: (*a*) to form the wound; (*b*) to serve as the dorsal wall for the poison canal; and (*c*) to hold the stylets in position. The stylet-sheath (*SH*) expands at its base to form the bulb of the sting (*B*) and the latter is prolonged inwards as a pair of diverging arms (*SHA*). The *stylets* or lancets (*S*) are each grooved along their entire length, and along the sheath are two guide-rails, which fit accurately into the stylet-grooves (Fig. 533). By means of this arrangement, the stylets are maintained in position and are permitted of no other than an up and down movement. The apices of the stylets and their sheath are provided with forwardly directed barbs. At their bases, the stylets diverge into a pair of arms closely associated with those of their sheath by means of a prolongation of the groove and rail device. Associated with the sting are three pairs of plates: the innermost or posterior pair is termed the inner or *oblong plates* (*OP*), which represent the divided ninth sternum and, attached to each, is the basal arm of the stylet-sheath of its side. Distally, the oblong plates carry a pair of *palp-like appendages* (*SP*). The two *triangular* or *fulcral plates* (*TP*) represent, according to Zander, the reduced sternum of the eighth segment and to each is attached the corresponding arm of a stylet. At its dorsal and posterior angle, the triangular plate is articulated with a large *outer* or *quadrate plate* (*QP*) and, at its ventral angle, with the oblong plate of its side. The quadrate plates represent part of the ninth sternum, the median portion of the latter region being probably seen in a membranous lobe (S_9.) which overlies the bulb of the sting.

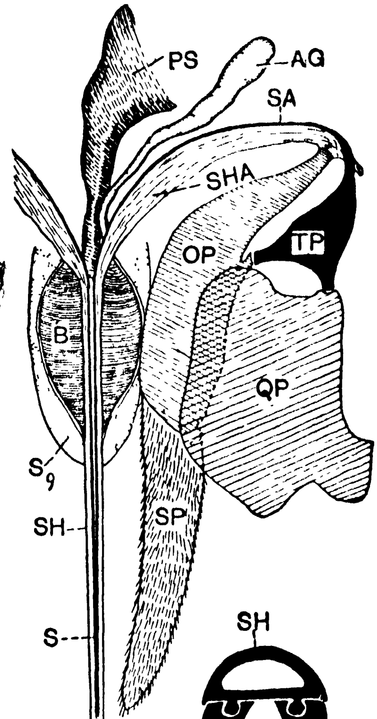

Fig. 533.—Diagram of the Sting (ventral view) of the Hive Bee with adjacent Sclerites of the left side: on the right side below is a transverse section of the Terebra.

AG, alkaline gland; *PC*, poison canal; *PS*, poison sac; for other lettering vide pp. 532–33.

The three pairs of plates already described function as levers, and powerful muscles are attached thereto. By means of the rotation of the fulcral and oblong plates, the sheath and its stylets are driven through the tissues of the victim when stinging takes place. The secretions of the two types of glands intermingle, and the fluid then finds its way down the canal formed by the sheath and the stylets, thus entering the wound made by the former. The structure of the ovipositor in certain Chalcidoidea has been shown by Imms (1918) to be essentially similar to that already described in the case of the honey bee, and in the Braconid *Doryctes* Seurat (1899) has found the same type of mechanism. In the Symphyta the stylets are adapted for sawing or boring and the sheaths remain separate and unfused.

Two sets of poison glands are found associated with the ovipositor, and are best developed when the latter organ is modified into a sting (Figs. 534, 537). A pair of filiform *acid glands* open, either separately or by means of a common duct, into a large poison-sac. Their secretion has an acid reaction and, in certain ants, contains formic acid. The poison-sac discharges into the anterior end of the bulb of the sting and, situated close to its opening, is the aperture of an unpaired *alkaline gland*, so called from the alkaline reaction given by its secretion. Experiments conducted by Carlet (1890) indicate that the full stinging properties are effected by a mixture of the secretions of the two types of glands. This observer found that certain Diptera die almost instantly when stung by the hive bee : the same species inoculated with the secretion of either kind of gland alone did not succumb for a considerable time, while a successive inoculation of the same individual first with the secretion from one gland, and then with that from the other, resulted in death in a much shorter time than in the case of an individual which had been inoculated from either gland alone. According to Bordas (1897), in the Ichneumonidæ the acid gland consists of numerous filiform tubes, and an accessory poison gland is present in those same insects and also in the Crabronidæ.

B. INTERNAL ANATOMY

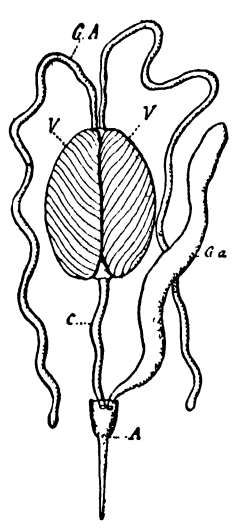

FIG. 534. — *VESPA GERMANICA*, POISON GLANDS.

GA, acid gland; *V*, poison sac with canal *c*; *Ga*, alkaline gland; *A*, terebra. *After* Bordas, 1897.

THE ALIMENTARY CANAL (Fig. 535) is of a tolerably uniform character throughout the order and presents but few notable deviations in its morphology (vide Bordas, 1894). In ants there is an *infra-buccal chamber* below the floor of the mouth : it takes the form of a spheroidal sac and opens into the mouth cavity by means of a short narrow canal. According to Wheeler (1910), this chamber is used by the ant as a receptacle for the fine particles of solid and viscous food, rasped off or licked up by the tongue. Any juices that may be contained in this nutriment are sucked back into the pharynx, and the solid residue thrown out as a pellet, which retains the form of the chamber in which it was moulded. The mouth-cavity leads into the *pharynx*, which is an organ of suction, and is moved by powerful dilator muscles. The *œsophagus* is a long narrow tube, especially in forms with an elongate petiole, but is relatively short in *Apis* and *Vespa*. Among the Aculeata the œsophagus dilates in the anterior portion of the abdomen into a thin-walled crop or *honey-stomach*. The latter is lined with a chitinous membrane and its walls contain muscle fibres : it serves as a reservoir for the liquid that has been imbibed, regurgitating it when required. In the repletes, or honey ants, the crop is remarkably distensible and, when full, largely determines the shape of the gaster. The crop is succeeded by the *proventriculus*, which is a very characteristic part of the gut in Hymenoptera and forms the neck-like region between the crop and true stomach. In *Apis* it is invaginated into the posterior wall of the crop, and has a X-shaped aperture provided with four triangular lips. The posterior opening of the proventriculus into the stomach is guarded by a well-developed valve. The function of the proventriculus, and its method of action, have given rise to discussion : it apparently serves to pump food from the crop into the stomach and, when closed, to prevent its regurgitation. The *stomach* or *ventriculus* is the largest part of the alimentary canal in *Apis* and *Vespa*, and is bent into a U-shaped loop. In the Crabronidæ, Sphegidæ, Formicoidea and the Parasitica it is reduced to a small elliptical chamber. In the female of *Doryctes*, which lives but a short time and takes no nourishment, its anterior portion has undergone atrophy

(Seurat). The food in most Hymenoptera is of a fluid nature and a *peritrophic membrane* is usually wanting. The structure described by Snodgrass (1910) in *Apis* is of a different nature, and consists of a matrix of secretion, in which are embedded a number of dismembered secretory cells, the whole mass separating from the underlying epithelium, and contracting around the food which it surrounds as a membrane. In most Hymenoptera, the *ileum* is a short simple tube but, in *Apis*, its length is much increased, and this region of the gut is looped upon itself. The *rectum* forms an enlarged terminal chamber, and its walls are furnished with three rectal papillæ in ants, four in *Doryctes* and six in *Apis* and most other Hymenoptera. Little is known of the physiology of the digestive system but a contribution to the subject has been made by Pavlovsky and Zarin (*Quart. Journ. Mic. Sci.*, 1922).

The *Malpighian tubes* are extremely variable in number and, in the Aculeata, they vary from 100 to 125 in the Vespidæ; from 20 or 30 in *Megachile* and its allies; and from 6 to 20 among ants. They all open separately into the ileum, and are often disposed in groups. Thus, in *Bombus* and *Apis* there are about 100 of these tubuli and, in the former genus, they are arranged in four bundles; in the Chrysididæ there are about 40 Malpighian tubes arranged in three bundles; and in the Eumenidæ they number from 40 to 70, which are disposed in two groups. Among the Parasitica, these organs are often much less numerous: in *Blastophaga* they number from 8 to 14 (Grandi), in *Doryctes* 9, in the Ichneumonidæ there are generally from 50 to 60, and in the Tenthredinidæ 20 to 25. Among hymenopterous larvæ there are four Malpighian tubes in *Apis* and the Formicoidea, but in most of the parasitic families there is only a single pair of these organs.

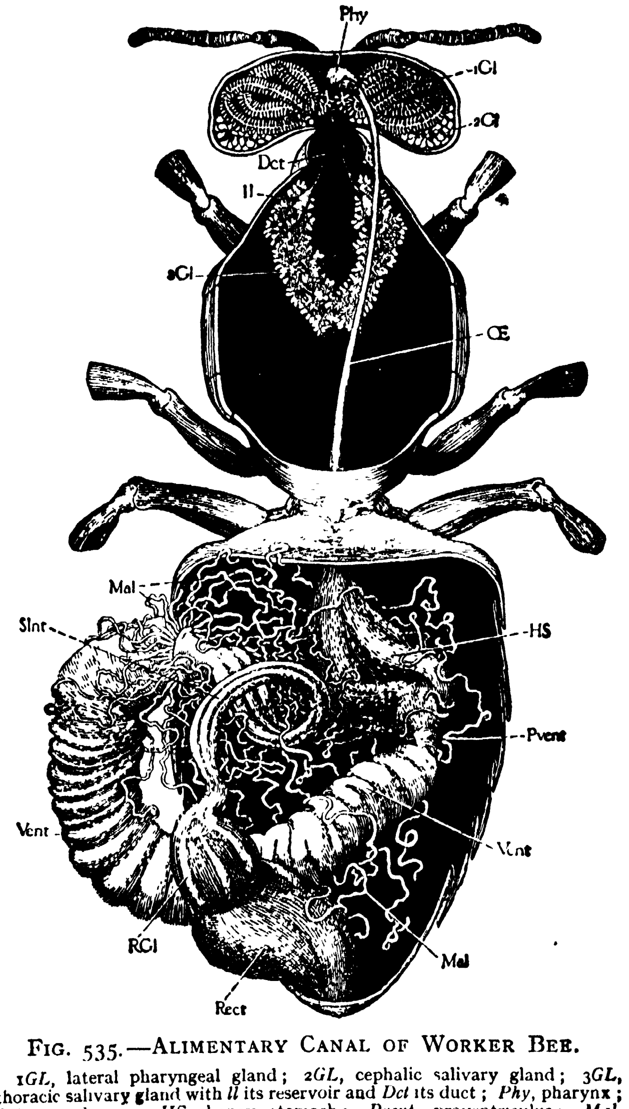

FIG. 535.—ALIMENTARY CANAL OF WORKER BEE.

1*GL*, lateral pharyngeal gland; 2*GL*, cephalic salivary gland; 3*GL*, thoracic salivary gland with *ll* its reservoir and *Dct* its duct; *Phy*, pharynx; *OE*, œsophagus; *HS*, honey stomach; *Pvent*, proventriculus; *Mal*, Malpighian tubes; *Vent*, ventriculus; *SInt*, small intestine; *Rect*, rectum and *RGl*, its papillæ. *After* Snodgrass, *U. S. Bur. Entom. Tech. Ser. Bull.* 18 (reduced).

SALIVARY GLANDS (vide Bordas, 1894, etc.) are well developed in the bee and consist of two pairs—one situated in the head and the other in the thorax (Figs. 535, 536). Their four ducts unite to form a common canal which opens on the hypopharynx. The *cephalic salivary glands* (post-cerebral glands of Bordas ; system No. 2 of Cheshire) lie against the posterior wall of the head. The *thoracic salivary glands* (system No. 3 of Cheshire) correspond with the ordinary salivary glands of most other insects. The contents of each gland are discharged into a reservoir, whose duct unites with its fellow to form the main salivary duct which, also, receives those of the cephalic glands. In the drones and queen there is a mass of gland cells situated just above the ocelli. These are the post-ocellar glands of Bordas but, according to Snodgrass, they are detached lobes of the cephalic glands. In addition to the foregoing, there is a pair of large *lateral pharyngeal glands* (supracerebral glands of Bordas ; system No. 1 of Cheshire) which are regarded by many authorities as being the source of the royal jelly, which is fed to the larval and adult queens and drones by the workers. Each is in the form of a long coiled chain of follicles packed away in the antero-dorsal region of the head ; these glands are absent in the drone and rudimentary in the queen. Opening into the floor of the pharynx, between the ducts of the lateral pharyngeal glands, is a transverse row of cells which forms the *ventral pharyngeal gland* of Snodgrass (sublingual gland of Bordas). A sac-like *mandibular gland* opens at the inner angle of each jaw : its function has not been ascertained, but it is larger in the queen than in the worker, and poorly developed in the drone. A second or *internal mandibular gland* has been described by Bordas in the worker of *Apis*, and also found in *Bombus* and *Vespa* : it is a delicate racemose mass, opening near the posterior inner edge of the mandible.

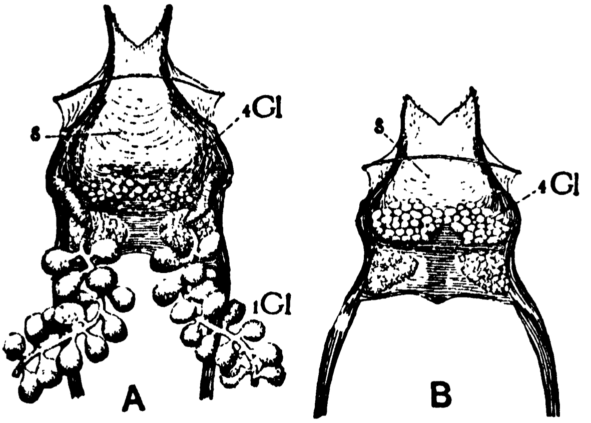

Fig. 536.—Pharyngeal Plate (S) and associated Glands of *A*, Worker and *B*, Drone of Hive Bee.

1GL, base of lateral pharyngeal gland; *4GL*, ventral pharyngeal gland. *After* Snodgrass, *loc. cit.*

THE HEART is well developed, and is usually composed of four or five chambers, with a corresponding number of pairs of alary muscles. In *Apis* the chambers are situated in the third to sixth abdominal segments and, in ants, in the fourth to eighth segments. The heart is continued forwards as the aorta which, in the bee, is folded into about eighteen loops in the region of the petiole. In the latter insect both dorsal and ventral diaphragms are well developed.

THE MUSCULAR SYSTEM has been principally worked out in ants ; it is one of great complexity and the reader is referred to articles by Janet, Lubbock, Berlese and others. In the deälated queens, among ants, the wing muscles are broken down by phagocytes, which take up and convert their substance, and somewhat later discharge it in the form of fat and albuminoid globules into the blood. In this manner the histolysis of the muscles provides nutrient material which contributes to the growth of the eggs (Janet).

THE NERVOUS SYSTEM.—The brain has been studied among the higher members of the order and more especially by von Alten (1910), Jonescu (1909), Kenyon (1896), Thompson (1913) and Viallanes (1886). It is principally characterized by the high degree of differentiation of the mushroom bodies and their related fibre-tracts. In ants, for example, there is considerable variation in their development, not only among different species, but also in different castes of the same species. According to Viallanes, the highest type of brain is found in *Vespa* where the calyces are complexly folded.

The ventral nerve cord is considerably less specialized than in the cyclorrhaphous Diptera. According to Brandt (1879) the most generalized condition is exhibited in the Tenthredinoidea where there are three thoracic and nine abdominal ganglia. Among the Apocrita the majority of the species similarly possess three thoracic ganglia, but among the Crabronidæ and Apoidea there are only two thoracic centres. The first is the prothoracic ganglion and the second is a complex formed by the fusion of the meos- and meta-thoracic and one, or more, of the abdominal ganglia. The second thoracic centre innervates the 2nd and 3rd pairs of legs, the wings, propodeum, and first abdominal segment. Six abdominal centres are present in many Ichneumonoidea and Formicoidea, also in *Ammophila, Cerceris, Odynerus,* and others. In most other Apocrita there are fewer abdominal ganglia, and the latter may be reduced to two centres as in the Cynipid *Dryophanta folii* (L.) Forst., or to a single centre, as in certain Chalcids. In the females of many Aculeata the last two abdominal ganglia are more or less fused: thus in *Mutilla europea* and *Megachile* there are five such ganglia in the latter sex and four in the male. In *Bombus* the worker and female have six ganglia and the male five. In the worker of the hive bee there are five ganglia, while the female as well as the male has but four. In *Vespa* the worker similarly has five ganglia, but the male and female are exceptional in having six. In *Blastophaga* there are two abdominal centres in the female, while in the male they are fused into a common mass (Grandi).

THE MALE REPRODUCTIVE SYSTEM.—The testes are separate in the Symphyta and also in *Apis* and *Bombus.* According to Bordas (1894) they are in close contact in *Vespa* and fused together in other Hymenoptera studied by him. Each testis is enclosed in a double membrane and may consist of 250–300 seminiferous tubuli as, in *Vespa, Bombus* and *Apis*; these tubuli are much less numerous in ants, and are usually reduced to three in other Hymenoptera. The vasa deferentia enlarge to form vesiculæ seminales which are usually cylindrical or sac-like in form. In *Vespa* and *Apis* they are particularly voluminous, while they are tubular and convoluted in *Athalia, Cimbex,* and *Bombus.* The two ejaculatory canals, which leave the vesiculæ, receive the ducts of a pair of accessory glands. The latter are large and sac-like in almost all members of the order. In *Apis* the ejaculatory canals are rudimentary, and the accessory glands open into the common ejaculatory duct.

THE FEMALE REPRODUCTIVE SYSTEM (Fig. 537). The ovaries are composed of polytrophic ovarioles; in *Apis* the latter are very numerous but their number is inconstant. In *Blastophaga* the ovarioles are very attenuated and closely packed together; according to Grandi there are 130–182 to each ovary. In *Cimbex* there are usually 20–30 ovarioles in each ovary; in *Aphelinus* there are five, while in other Chalcids and in the Ichneumonoidea there are commonly four. In *Doryctes,* however, each ovary is greatly developed and consists of a single pair of ovarioles; in *Aphidius* the latter are wanting and the follicles are simply enclosed in a sac-like membrane. Among ants the number varies, in different genera and species, between two (*Leptothorax emersoni*) and about 250 (*Eciton schmitti*) : in the workers, however, the number is very much lower, there is often a single ovariole to each ovary and rarely there are as many as twelve. The two oviducts unite to form the vagina and, in *Apis*, the latter is dilated posteriorly as the bursa copulatrix. A median spermatheca is generally present together with a pair of colleterial glands : the latter may open into a median reservoir as in *Cimbex* (Severin) or into the duct of the spermatheca as in *Apis.*

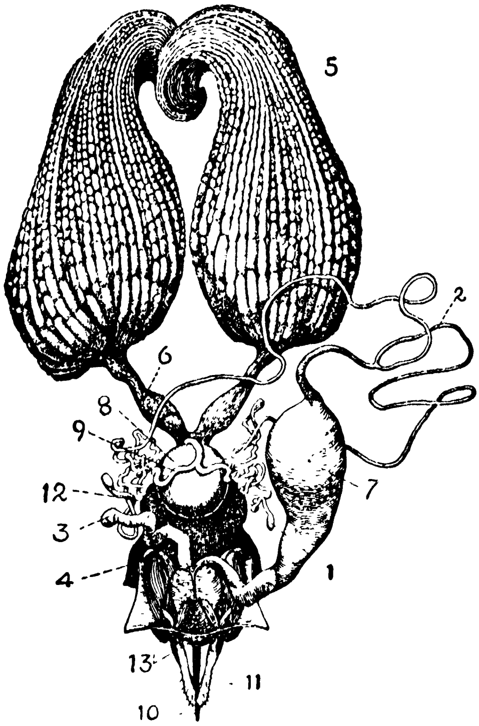

FIG. 537.—REPRODUCTIVE ORGANS, ETC., OF QUEEN BEE.

1, acid gland and 2, its duct ; 3, alkaline gland ; 4, bursa copulatrix ; 5, ovary ; 6, oviduct ; 7, poison sac ; 8, spermatheca and 9, its gland ; 10, terebra ; 11, sting palp ; 12, vagina ; 13, 9th sternum Adapted from Snodgrass, *loc. cit.*

Metamorphoses

THE EGG

The eggs of Hymenoptera are usually ovoid or sausage-shaped and, in the parasitic groups, they are frequently provided with a pedicel. The latter structure may arise from either pole of the egg (Adler) and is of very general occurrence among the Cynipoidea. In the gall-forming species of the latter group it may be five or six times the length of the egg itself. Stalked eggs are also found among the Chalcidoidea and Proctotrypoidea : in *Blastophaga* the pedicel may measure more than twice the length of the egg. In the majority of cases the function of this appendage is obscure, but in *Blastothrix* it protrudes through the body-wall of the host, and functions as a kind of respiratory funnel, which enables the newly hatched larva to breathe the outside air (vide Imms, 1918). In *Schedius kuvanæ* the eggs are deposited within those of the gipsy moth, with their pedicels protruding to the exterior (Howard and Fiske), and it is probable that the latter organs fulfil a similar function in this instance also. A reduced pedicel is found in other Chalcids as well as in certain of the Ichneumonoidea ; it is met with both in the case of eggs which are laid externally to their hosts, and in those which are laid within the latter.

THE LARVA

A typical hymenopterous larvæ is composed of a well-developed head, three thoracic and usually nine or ten abdominal segments. With few exceptions the tracheal system is peripneustic or holopneustic, either throughout life or in the later instars. Among the Symphyta the head is strongly chitinized and there are powerful biting mouth-parts. Three pairs of thoracic limbs and six or eight pairs of abdominal feet are generally present. Such larvæ feed upon plant tissues, and are peripneustic or holopneustic throughout life, with nine or ten pairs of spiracles. Larvæ which bore into stems or wood have lost the abdominal feet, but retain the thoracic limbs usually in a more or less reduced condition. Among the Apocrita, the larvæ are apodous: evanescent thoracic appendages are present, however, in *Eucoila*, and a single pair is found in larvæ of the Platygasteridæ, and in these instances they are probably modified survivals of true appendages. As a general rule, the larvæ of the Apocrita (Fig. 538) are maggot-like in form; the head is less strongly chitinized than in the Symphyta, and in the parasitic forms it is often greatly reduced and sunk into the prothorax. Degeneration of the organs of special sense is very evident and, in most cases, the larvæ are sluggish and move but little. These features are associated with the fact that their possessors live in darkness, and are supplied with an abundance of nutriment in their immediate vicinity, there being no necessity to seek for it. Definite ocelli are wanting, and the antennæ are reduced to short sensory processes, small papillæ, or may be atrophied. The mandibles may be either dentate, sickle-shaped or simple pointed spines with broad flattened bases. The labrum, maxillæ and labium are fleshy lobes, and the two last-mentioned organs exhibit little or no differentiation into separate sclerites. Both the maxillary and labial palpi are usually represented by small papillæ or are totally wanting. In almost all the larvæ of the Apocrita the stomach is a blind sac and does not communicate with the hind intestine until the final instar, the fæcal contents only being evacuated at the conclusion of the larval stage. Well-developed salivary glands are present, often of considerable length, and the ganglia of the ventral nerve cord are often undifferentiated. In the Aculeata the tracheal system is holopneustic throughout life and generally ten pairs of spiracles are present. In the Parasitica the respiratory system undergoes profound modifications in correlation with varying modes of life (vide Seurat 1890). Thus, among the ectoparasitic species (Fig. 539) the larvæ are hatched with a peripneustic tracheal system but the full number of spiracles is not always acquired until later in life. The typical number of spiracles is nine pairs but they are not always borne on the same segments in different species. The Chalcid *Aphelinus* has eight pairs of spiracles and the Ichneumon *Pimpla pomorum* has ten pairs. In the Proctotrypid *Lygocerus* the larva is hatched with two pairs and there are seven pairs in the last instar. Among the endoparasitic forms the young larvæ are

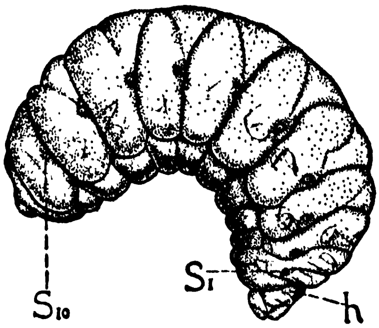

FIG. 538.—LARVA OF A BEE: ENLARGED.

h, head; *s*, spiracles. From Nelson.

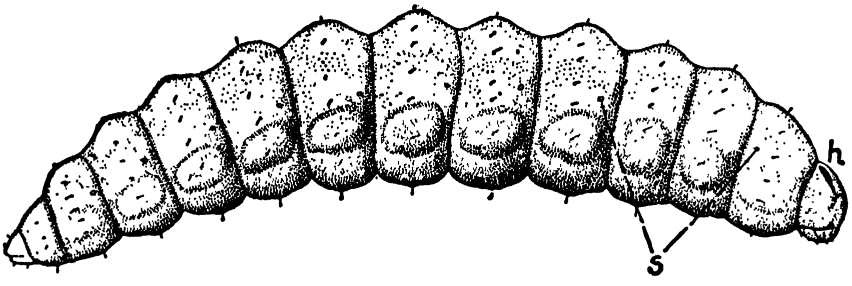

FIG. 539.—FULLY-GROWN LARVA OF AN ECTOPARASITIC ICHNEUMON, *PIMPLA POMORUM*: ENLARGED.

h, head; *s*, spiracles.

commonly apneustic, but this condition is rarely retained throughout life. In the apneustic condition the cuticle is extremely thin and admits of the interchange of gases by means of diffusion. At this stage the larva is hæmophagous but it subsequently becomes carnivorous, devouring the various internal organs of its host. When it assumes this mode of life, a certain number of spiracles open on the surface of the body, and in the final instar there are usually nine pairs present (vide Thorpe, 1932).

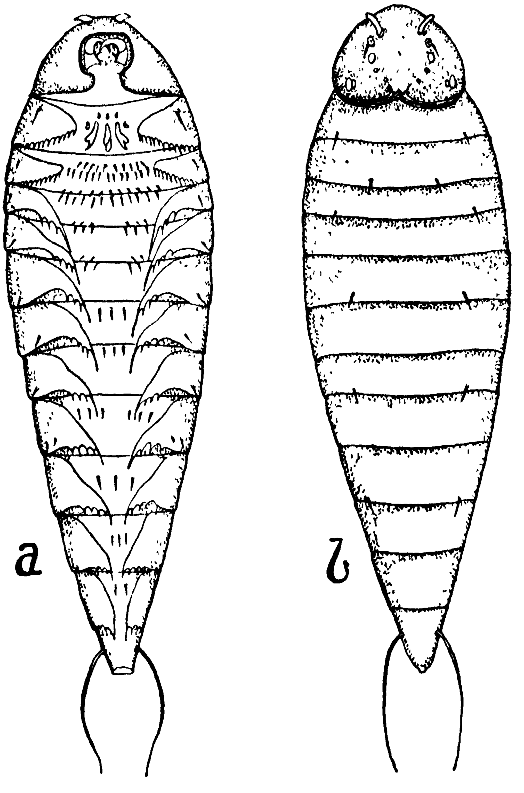

FIG. 540.—PLANIDIUM OF *PERILAMPUS*.

a, ventral; *b*, dorsal. *After* H. S. Smith, *U. S. Bur. Ent. Tech. Ser.* 19, pt. 4.

Hypermetamorphosis occurs among many of the Parasitica and examples of this type of development are known in five of the major divisions of the order (vide Richardson, 1913). At least ten distinct primary larval forms are known in addition to the usual larval type already described. Any attempt at the classification of these forms at present can only be a tentative one pending the growth of more detailed knowledge. The principal types of primary larvæ are as follows (Figs. 540, 541). (1) The PLANIDIUM (Fig. 540) is an active larva invested with strongly chitinized imbricated segmental plates and provided with spine-like locomotory processes. It develops from an egg which is laid away from the host and is a migratory form adapted to seek out the latter. This type is known in the Chalcid genera *Orasema, Perilampus, Leucospis* and, in a modified form, in *Spalangia*. (2) The CAUDATE TYPE is well exhibited in certain Ichneumonidæ, Braconidæ, and in a few of the Chalcidoidea, notably *Encyrtus aphidivorus*. It is somewhat vermiform in shape with a caudal outgrowth of variable length (vide also p. 571). (3) The CYCLOPOID OR NAUPLIIFORM TYPE occurs in certain of the Proctotrypoidea. It is characterized by the large swollen cephalothorax, very large sickle-like mandibles and a pair of bifurcate caudal processes of variable form. In its general facies it bears a resemblance to the nauplius of Crustacea. (4) The TELEAFORM TYPE is found in certain other Proctotrypoidea and in several of the Chalcidoidea; it derives its name from the primary larva of *Teleas*. The cephalic extremity is prominently hooked or curved; posteriorly the body is prolonged into a caudal process, and the trunk is armed with one or more girdles of setæ. Apparently modified examples of this larval type have been described by McColloch in *Eumicrosoma* and by Silvestri in the Chalcids *Poropœa* and *Anaphoidea*. (5) The VESICLE-BEARING TYPE occurs in *Apanteles* and *Microgaster* and is characterized by the proctodæum being everted to form a swollen anal vesicle. (6) The EUCOILIFORM TYPE is known in the *Figitidæ*: it differs from the teleaform type in possessing three pairs of long thoracic appendages, and in the absence of the cephalic process and the girdles of setæ. (7) The POLYPOD TYPE, with 8 to 12 pairs of trunk appendages, occurs in *Ibalia*, the Braconid *Microdus* and in *Phænoserphus*: in *Eucoila* and allies it follows the protopod stage. The subsequent stages in development in those species in which hypermetamorphosis occurs exhibits wide variation: thus the second larval instar of *Teleas* is of the cyclopoid type, but the final instar in all cases is the ovoid maggot-like type of larva characteristic of the Apocrita.

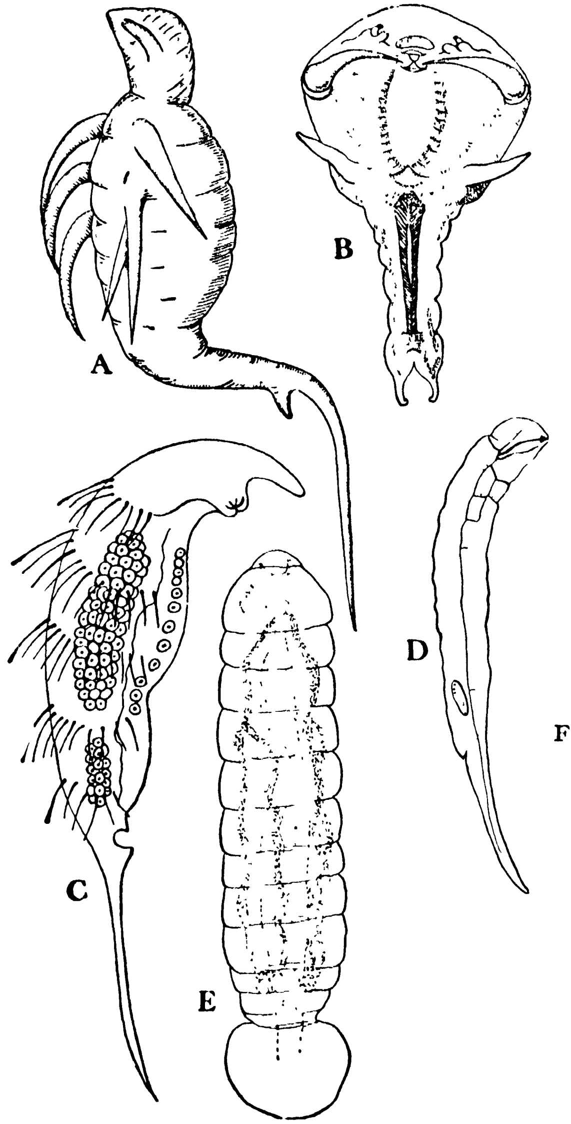

FIG. 541.—PRIMARY LARVÆ OF VARIOUS PARASITIC HYMENOPTERA.

A, eucoiliform (*Eucoila*); *after* Keilin and Pluvinel. *B*, cyclopoid (*Trichacis*) *after* Marchal. *C*, teleaform (*Teleas*), *after* Ayers. *D*, caudate (*Mesochorus*), *after* Seurat. *E*, vesicle-bearing (*Microgaster*), original. All highly magnified.

The presence of a trophic membrane or trophamnion (Fig. 542) enclosing the embryo in certain endoparasitic Hymenoptera, has been already alluded to (p. 176). It has been found in diverse species, comprising members of each of the main parasitic groups, but is evidently not homologous in all cases, and very different methods of formation have been described. This membrane is believed to play an important part in the nutrition of the embryo.

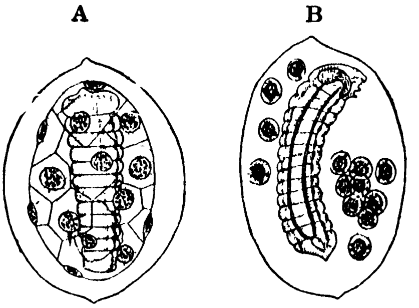

FIG. 542.—*CHALCIS* (*SMICRA CLAVIPES*. *A*, EGG WITH EMBRYO SURROUNDED BY TROPHAMNION. *B*, YOUNG LARVA AND DISINTEGRATED TROPHAMNION.

After Henneguy "Les Insectes."

THE PUPA

In the Apocrita the prepupa is well defined and is intermediate in its characters between the larva and pupa (Fig. 205). The prothoracic segment is distended by the developing pupal head, the wings and legs have assumed the form of those of the pupa, and it is in this stage that the first abdominal segment or propodeum becomes incorporated with the thorax. After the final larval moult, the prepupa passes into the pupa and the latter is of the exarate type, in which the wings and appendages are free and not soldered to the surface of the body (Fig. 202). With the exception of the Cynipidæ and Chalcidoidea a cocoon, though often slight, is of general occurrence in the order. In many Tenthredinoidea it is parchment-like ; in others it is formed of agglutinated soil particles ; while in *Cimbex* the cocoon is formed of an outer and inner coat, and attains a higher degree of development than in other Hymenoptera. In many of the Aculeata the cocoon is little more than a silken lining to the larval cell, and in some of the ants it is totally wanting. Among the Braconidæ dense masses of silken cocoons are often formed by the members of a species which issue from a single individual host.

Classification of Hymenoptera

The Hymenoptera are divisible into the sub-orders Symphyta and Apocrita. It has long been customary and convenient to separate the Apocrita into two main divisions, viz. the Aculeata or stinging forms and the Parasitica (Terebrantia), which are parasites of other insects. It is not, however, easy to find clear distinctions between these divisions, but the trochanters are typically 1-jointed in the Aculeata and most usually 2-jointed in the Parasitica. Biologically, the two divisions intergrade since a number of the Parasitica are plant feeders, while some Aculeata are parasites. In the Aculeate families Sapygidæ, Dryinidæ and Chrysididæ, the ovipositor retains its egg-laying function as in the Parasitica : in the other Aculeates, the ovipositor is converted into a sting and the egg-passage opens to the exterior at its base. The Aculeata fall very naturally into two great series, the Vespiformia and the Spheciformia. The former include the Vespoidea, or true wasps and their allies, together with the Formicoidea or ants. The Spheciformia comprise those solitary wasps which form the superfamily Sphecoidea, together with the Apoidea or bees. Structurally the Vespiformia are characterized by the lateral extensions of the pronotum reaching the tegulæ, whereas in the Spheciformia the sides of the pronotum form well-rounded lobes that are remote from the tegulæ.

The standard works on European Hymenoptera are those of André (1879, etc.) and Schmiedeknecht (1930) : for a synonymic catalogue of the species of the world vide Dalla Torre (1892–1902).

Sub-order I. SYMPHYTA

(Phytophaga, Sessiliventres or Chalastogastra).

ABDOMEN BROADLY SESSILE WITH NO MARKED CONSTRICTION AT ITS BASE ; TROCHANTERS 2-JOINTED. LARVÆ WITH THORACIC AND GENERALLY ABDOMINAL FEET.[1]

This sub-order includes the TENTHREDINOIDEA and ORYSSOIDEA (p. 565).

Sub-order II. APOCRITA

(Heterophaga, Petiolata or Clistogastra).

ABDOMEN NEVER BROADLY SESSILE, SEPARATED FROM THORAX BY A DEEP CONSTRICTION OR A PETIOLE : TROCHANTERS 1- OR 2-JOINTED. LARVÆ APODUS.

1 (10).—Hypopygium entire, closely united with pygidium:
oviposítor issuing from apex of abdomen.
2 (9).—Trochanters 1-jointed.

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[1] Except in *Oryssus.*

3 (6).—Pronotum extending back to tegulæ or latter absent. (*Vespiformia.*)
4 (5).—Petiole with one or two nodes. FORMICOIDEA (p. 585)
5 (4).—Petiole simple. VESPOIDEA* (p 595)
6 (3).—Pronotum not extending back to tegulæ. (*Spheciformia.*)
7 (8).—Hind tarsi slender: pubescence simple. SPHECOIDEA[1] (p. 602)
8 (7).—Hind tarsi dilated or thickened: pubescence of head and thorax feathery or plumose. APOIDEA* (p. 605)
9 (2).—Trochanters 2-jointed. PROCTOTRYPOIDEA (p. 582)
10 (1).—Hypopygium divided, or not closely united with pygidium: ovipositor issuing some distance before apex of abdomen.
11 (14).—Pronotum extending back to tegulæ: antennæ not elbowed: trochanters 1- or 2-jointed.
12 (13).—Fore-wings without a stigma: trochanters usually 1-jointed. CYNIPOIDEA (p. 579)
13 (12).—Fore-wings with a stigma: trochanters 2-jointed. ICHNEUMONOIDEA (p. 570)
14 (11).—Pronotum not extending back to tegulæ: antennæ elbowed: trochanters 2-jointed. CHALCIDOIDEA (p. 573)

Superfamilies indicated * form the division Aculeata—the remainder constitute the Parasitica.

Sub-order I. SYMPHYTA

Included in this division are all the more primitive members of the Hymenoptera which are recognized by the broadly sessile abdomen and the fact that its first segment is only partially amalgamated with the thorax. The imagines do not exhibit the highly specialized habits and instincts so prevalent among the Apocrita and the ovipositor is adapted for sawing or boring: except in *Oryssus* parasitism is wanting. The larvæ (vide Yuasa, 1922) have a well developed head and 13 trunk segments: three pairs of thoracic legs and frequently 6 or more pairs of abdominal limbs are present. The tarsus and claw of each thoracic leg are fused into a single piece while the abdominal limbs are devoid of crochets. A single pair of ocelli is present and the maxillary and labial palpi are usually 4- and 3-jointed respectively. Spiracles are always present on the prothorax and first eight abdominal segments: metathoracic spiracles are also present in the Cephidæ, and in *Sirex* and *Tremex*, but are vestigial or wanting in the larvæ of other Symphyta.

The Symphyta are divisible into two superfamilies and eight families as given below.

1 (2).—Antennæ inserted below the clypeus and eyes, and beneath a frontal ridge: propodeum not divided. With a single family ORYSSIDÆ. **Oryssoidea** (p. 569)
2 (1).—Antennæ inserted above the clypeus: propodeum medianly divided. **Tenthredinoidea** (p. 566)
3 (6).—Anterior tibial spurs single: prothorax large.
4 (5).—Pronotum truncated behind: middle lobe of mesonotum not reaching scutellum: ovipositor very short. CEPHIDÆ (p. 566)
5 (4).—Pronotum strongly curved or emarginate behind: middle lobe of mesonotum reaching scutellum: ovipositor long and powerful. SIRICIDÆ (p. 566)

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[1] In many Chrysididæ and some Bethylidæ the pronotum does not extend back to the tegulæ. In the Trigonalidæ the trochanters are 2-jointed.

[2] In the Pelecinidæ the trochanters are 1-jointed.

6 (3).—Anterior tibial spurs two.

7 (8).—Radial cell in fore-wing divided by cross-vein: 3rd antennal joint longer than following joints together. XYELIDÆ (p. 568)

8 (7).—Radial cell not divided by cross-vein: 3rd antennal joint not longer than the following joints together.

9 (10).—Hind margin of pronotum straight or nearly so: fore-wing with subcostal vein distinct. PAMPHILIIDÆ (p. 568)

10 (9).—Hind margin of pronotum deeply emarginate: fore-wing with subcostal vein absent or vestigial.

11 (12).—Antennæ clubbed: abdomen with separate pleural sclerites. CIMBICIDÆ (p. 568)

12 (11).—Antennæ not clubbed: abdomen without separate pleural sclerites. TENTHREDINIDÆ (p. 568)

A. Superfamily **Tenthredinoidea**

FAM. CEPHIDÆ (Stem Saw-flies).—The Cephidæ are a small family of slender, narrow-bodied insects with a thin integument (Fig. 543). The prothorax is exceptionally large and movably articulated with the following segment. They are mostly black or darkly coloured, either with or without narrow yellow bands. In length they seldom measure more than 18 mm. and are usually smaller. The larvæ bore into the stems and shoots of various plants and are apodous, with the exception of three pairs of reduced tubercle-like thoracic limbs. They are also characterized by the vestigial ocelli, the well developed metathoracic spiracles and the presence of vestigial sub-anal appendages. The abdomen terminates in a small retractile point or spine which arises from a fleshy protuberance on the last segment, above the anus. The pupæ are usually enclosed in transparent cocoons within the stems of the food-plant. For an enumeration of the larval characters in different genera vide Middleton (*Proc. Ent. Soc. Washington* 19, 1917). Less than a dozen species occur in the British Isles, the best known being *Cephus pygmæus* L., the Wheat-stem Borer. Although destructive in many parts of Europe, and introduced into N. America, it is rarely injurious in Britain. The eggs of this species are laid in the stem of the wheat plant, and the larva bores its way upwards through the latter, ultimately weakening it below the ear: for an account of its biology and parasites see Salt (*Bull. Ent. Res.* 1931). *Janus* (*Phyllæcus*) *flaviventris* Fitch lays its eggs in the centre of the pith of the shoots of currants and its larvæ bore through the stems: its metamorphoses are figured by Marlatt (*Ins. Life*, 7).

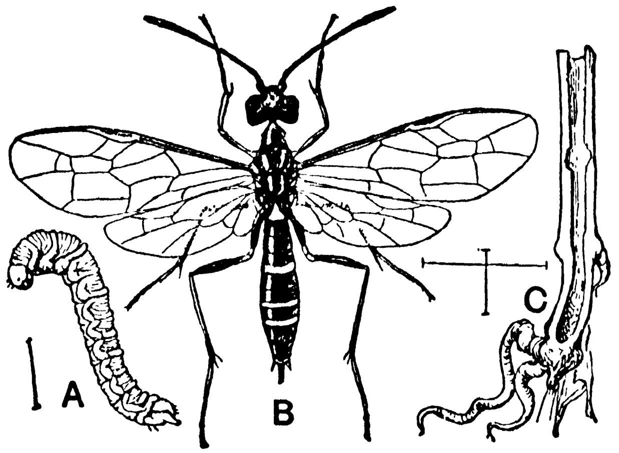

FIG. 543.—*CEPHUS OCCIDENTALIS.*

A, larva; *B*, female; *C*, larval gallery in grass-stem. *After* Marlatt, *U.S. Dept. Agric.*

FAM. SIRICIDÆ (**Uroceridæ**: Wood-wasps or Horn-tails).—A family of large-sized insects with conspicuous coloration, being often black and yellow or metallic blue. The abdomen usually terminates in a spine or horn, which is short and triangular in the males and lanceolate in the females. The ovipositor is exceedingly strong and, when at rest, projects backwards in the horizontal plane, and has the appearance of a powerful sting. This instrument is used for boring and drilling, and not for sawing as in the Tenthredinidæ. Holes are made through the bark into the new wood of various forest and shade trees and a single egg is deposited in each hole. The larvæ on hatching burrow into the heart wood and often cause considerable damage. Pupation takes place in the larval gallery and a cocoon of silk and gnawed wood is constructed. The larva has a tolerably large head and three pairs of reduced thoracic limbs; the last trunk segment terminates in a horny process which aids in locomotion. The best known species in the British Isles is *Sirex gigas* which lives in Coniferæ, and its life-history appears seldom to occupy less than two years. It usually only attacks trees which have passed their full vigour and are not perfectly healthy, but sound felled trees are sometimes selected. The metallic blue *S.* (*Paururus*) *noctilio* F. is also not infrequently met with, but it is difficult to say whether either species is truly indigenous. For further information on the British species of the genus, see Chrystal (*Bull. Ent. Res.* 19, 1927). In the allied genus *Tremex* the larva affects broad-leaved trees in N. America. *Xiphidria* differs from *Sirex* and its allies in the absence of the spine from the apex of the abdomen : its larvæ burrow in the wood of *Alnus, Salix,* etc., and two species occur (rarely) in Britain (vide Chrystal and Skinner, *Scot. Forest. Journ.* 1932). The genera of the family have been monographed by Konow (*Gen. Insectorum* 28).

The next four families were formerly grouped into a single family, the Tenthredinidæ (*sensu lat.*), and their species are known as saw-flies since the females are provided with a saw-like ovipositor. The antennæ are, perhaps, more variable in character than in any other family of insects, and often exhibit marked sexual differences. The most frequent number of joints is nine, but in *Hylotoma* there are only three, while in *Pamphilius* Latr. (*Lyda F.*) their number may exceed 40. In *Cimbex* and its allies the antennæ are clavate, in *Lophyrus* they are deeply pectinated in the males, and the third joint in the male is bifurcate and shaped like a tuning-fork. Two curious organs known as *cenchri* are situated one on each side of the middle of the mesothorax ; they are pale coloured membranous areas whose function does not appear to have been ascertained. Saw-flies are usually to be obtained by shaking the foliage of bushes and trees ; many frequent flowers and some are carnivorous, preying upon small Coleoptera and Diptera. Great variation exists as to the proportion of individuals of the sexes and in only a few species are the males as numerous as the females. Cameron has shown that in one-third of the British species males are unknown. Parthenogenesis occurs somewhat extensively in this family and in some species males, in others females, and in a third group individuals of both sexes are produced from unfertilized eggs. Thus in *Nematus* (*Pteronus*) *ribesii* only males have been reared from the unfertilized eggs. The impregnated females give rise to individuals of both sexes, but females predominate. In *Crœsus varus* and *Pœcilosoma luteolum* the parthenogenetic eggs produce females, and there is no indubitable case of males arising in this manner. For further information on the subject of parthenogenesis in this family vide Enslin (1914).

The eggs are usually laid in young shoots or in leaves and the saw, or cutting instrument, of the ovipositor is toothed in various ways in conformity with the nature of the oviposition. Its serrations are large and stout in species which lay their eggs in woody twigs ; very fine in those which oviposit in leaf-tissue ; or scarcely evident at all in *Nematus ribesii,* which simply attaches its eggs each by means of a small flange into a minute slit on the underside of a leaf. In most species, during oviposition the blades of the ovipositor move alternately, one being thrust forward while the other is withdrawn, until an incision or pocket of the required depth is formed. In structure the ovipositor differs from that of the Apocrita since the two valves forming the stylet-sheath remain separate but closely opposed, although not fused. Both the stylets and their sheath are more or less complexly serrated towards their apices while the 3rd pair of valves (outer gonapophyses of 9th segment) serve to protect the whole terebra. The larvæ are termed caterpillars and often bear a close general resemblance to those of the Lepidoptera. They are exclusively phytophagous in habit and affect almost all orders of Phanerogamia and certain of the Filices. Trees and bushes, however, support a larger number of species than herbaceous plants. The larvæ (Yuasa 1922) exhibit much diversity of habit and a large number are nocturnal feeders : many are solitary while others are gregarious. The vast majority live exposed, but some live internally in stems, fruit or galls and a certain number are leaf-miners. Many closely simulate their environment and are cryptically coloured, while others are very conspicuous with bright colours. In numerous species the larvæ are covered with a whitish powdery exudation : in *Caliroa* they are slug-like and the body is obscured by a darkly coloured slime or exudation and some species of *Blennocampa* are invested with bifurcate spines. The body-segments of saw-fly larvæ are usually subdivided, by means of transverse folds, into annulets whose number appears to be constant for each species (Fig. 544). Three pairs of thoracic limbs are present and almost all species carry abdominal feet also. Unlike those of the Lepidoptera there are usually more than five pairs of the latter organs and they are devoid of crochets. The number of these appendages varies among different sub-families. The Xyelidæ are exceptional in that they are borne on all the abdominal segments: in other families abdominal feet are absent from the 1st and 9th segments and in the Pamphiliidæ they are wanting on all segments. The head is large and sclerotized and there is a single ocellus on either side (Fig. 545). The antennæ are composed of a variable number of joints, attaining a maximum of seven in the Xyelidæ and Pamphiliidæ. In the latter family there are 3-jointed sub-anal appendages which are wanting in other families. In many cases the larvæ emit secretions which are produced by special glands. The latter in Cimbicidæ open just above the 2nd to 8th abdominal spiracles and in some instances eject a jet of spray. *Caliroa* has a pair of ventral digit-like glands opening between the head and prothorax: many larvæ are provided with glands resembling osmeteria, which open by means of a slit-like aperture on the sternum of each of the first 7 abdominal segments. Pupation, as a rule, takes place in an elongate-oval silken cocoon which may or may not be mixed with soil particles; in other cases an earthen cell is constructed.

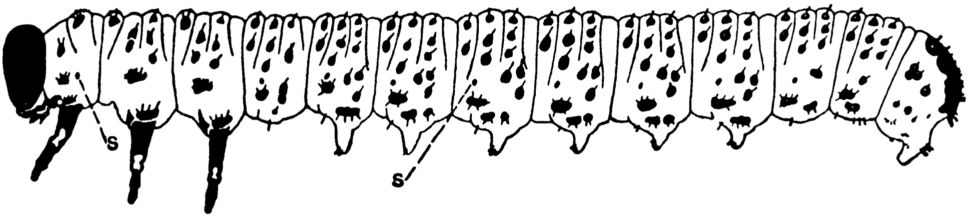

FIG. 544.—LARVA OF *NEMATUS RIBESII.*

s, spiracles. *After* MacGillivray, *Can. Entom.* 45.

FAM. XYELIDÆ.—This family has the most generalized venation among Hymenoptera (Fig. 530). The larvæ are also noteworthy since they retain feet on all the abdominal segments. The imagines may be easily recognized by the greatly elongated 3rd antennal joint: the ovipositor is moderately or very long. *Xyela* and *Macroxyela* are typical genera: the only British species, *X. juliæ*, is a rarity.

FAM. PAMPHILIIDÆ.—These are robustly-built insects with a short ovipositor and a primitive venation (Fig. 529). The larvæ (Fig. 545), on the other hand, have no abdominal feet: they are sometimes gregarious and often live in webs or rolled leaves. *Neurotoma* and *Pamphilius* are British genera: their species are rather infrequent in occurrence.

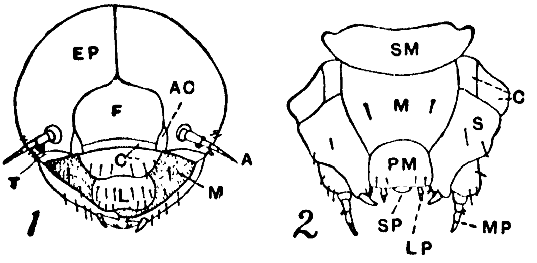

FIG. 545.—*PAMPHILIUS DENTATUS*, LARVA. 1, FRONTAL VIEW OF HEAD; 2, MAXILLÆ AND LABIUM.

AC, ante-coxal piece of mandible; *SP*, spinneret (other lettering as in Fig. 4 (p. 15) and Fig. 8 (p. 19). Adapted from MacGillivray, *loc. cit.*

FAM. CIMBICIDÆ.—In this family are the largest of all the saw-flies: many are almost massive in form, often conspicuously coloured or even metallic. They are easy to recognize by means of their clubbed antennæ and the ovipositor hardly extends beyond the apex of the abdomen. The larvæ have eight pairs of abdominal feet and the cocoons are commonly double, the outer one being of a leathery consistency. Characteristic genera are *Cimbex*, *Trichiosoma* and *Arge*.

✓ **FAM. TENTHREDINIDÆ.**—A very large family of moderate-sized species which comprise about 80 per cent. of all the Symphyta. The larvæ never have more than eight pairs of abdominal limbs and these are located on segments 2–7 and 10, or on 2–8 and 10 and rarely on 2–6 and 10. In the gall formers the legs are commonly reduced. During their larval stage some species are capable of causing great destruction of foliage and are thereby injurious. In this way *Nematus ribesii* is destructive to *Ribes*, various species of *Lophyrus* are injurious to pines, *Lygæonematus erichsonii* is sometimes exceedingly destructive to larch and *Caliroa cerasi* L. (*limacina* Retz.) to pear. (Species of several genera, notably *Pontania*, form galls, particularly upon the leaves of *Salix*. Beyerinck (*Botan. Zeit.* 46) has made a study of the development of the galls produced by *Pontania proxima* Lep. (*Nematus capreæ*). Unlike what happens in the case of Cynipid galls, those produced by this insect very quickly commence to develop and may be fully grown before the larva hatches. The cause of the gall is stated to be an albuminous secretion that is injected along with the egg into the tissue of the leaf, and Beyerinck suggests that it contains an enzyme that acts upon the plant cells in such a manner as to lead to gall formation. It appears that, in this case, it is the secretion and not the presence of the egg that is the primary cause, since after the egg has been killed by puncturing with a fine needle the gall continues to develop. In the case of *P. viminalis* Htg. Beyerinck finds that the galls produced by this insect fall to the ground during winter, but have the property of independent existence. In the spring they increase in size, develop additional chlorophyll and also produce lenticels.

B. Superfamily **Oryssoidea**

FAM. ORYSSIDÆ.—This very small family is evidently a relic of an ancient group, and is distributed over most parts of the world. It is represented in Europe and N. America by the single genus *Oryssus* and the species *O. abietinus* has occurred rarely in Britain. Structurally the members of this family show features belonging to both the Symphyta and Apocrita. The wings have a reduced venation (Fig. 546) quite unlike that of any Symphyta, since there are no closed submarginal cells in the hind-wing, while the divided anal cell of the fore-wing is not found in any Apocrita. In the position of the antennæ, and the form and attitude of the long ovipositor when at rest, the family is unique among Hymenoptera. The only known larva is an apodous ectoparasite of Buprestidæ. It is described by Rohwer and Cushman (*Proc. Ent. Soc. Washington*, 19, 1917), who also emphasize the unique features of the family. On account of its adult characters, and the form and habits of the larva, they place the family in a separate sub-order, the *Idiogastra*—intermediate between the Symphyta and Apocrita. It is, however, retained here in the Symphyta since the abdomen is broadly attached to the thorax, as in all members of the sub-order.

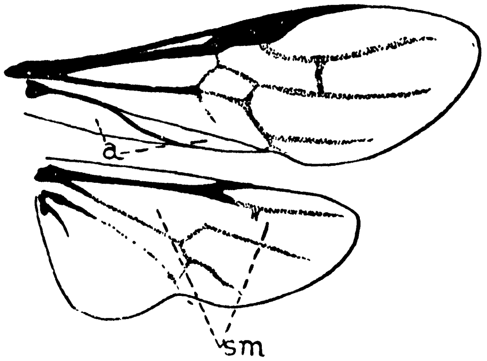

FIG. 546.—RIGHT WINGS OF *ORYSSUS ABIETINUS.*

a, divided anal cell; *sm*, submarginal area. Adapted from MacGillivray.

One of the best general accounts of the Symphyta is that of Enslin (1914), which contains a full bibliography: among monographic works that of Konow (*Gen. Insectorum*, 27, 29) is important. The British Symphyta are dealt with by Cameron (1882–92) and a useful aid to their identification is given in the more recent series of articles by Morice (*Ent. Month. Mag.* 1903 onwards).

Sub-order II. APOCRITA

Included in this sub-order are the vast majority of Hymenoptera, all of which are recognizable by the abdomen being basally constricted or petiolate. The imagines are almost always highly specialized in their habits and are often social, living in large communities. The ovipositor is adapted for piercing in the Parasitica and usually for stinging in the Aculeata. The larvæ are apodous, and the head is generally well developed but, among certain of the parasitic families, it is greatly reduced. The larval habits are extremely diverse. Thus many of the Cynipoidea and a few of the Chalcidoidea are phytophagous. Other of the Cynipoidea, all the Ichneumonoidea, and almost all the Chalcidoidea, are carnivorous, being either ecto- or endoparasites. The Sphecoidea and Vespoidea are largely predaceous, and the Apoidea are nourished upon nectar and pollen.

The British Aculeata are described and figured in the work of Saunders (1896). Among the Parasitica, the Cynipoidea are dealt with by Cameron (1882–92) and the Ichneumonoidea by Marshall (1885–99) and Morley

(1903–14), but no monographic works exist on the remaining British parasitic groups.

The literature on the biology of the Aculeata has assumed enormous proportions. Among the more important works are those of Fabre (1879–91), Ferton (1901–21), Friese (1922–23), G. W. and E. G. Peckham (1898), Roubaud (1916), Grandi (1926–31), Williams (1919), and Wheeler (1910). The latter authority (1923) has given an admirable annotated bibliography of the subject to which the reader is referred.

Superfamily **Ichneumonoidea** (Fig. 547)

ANTENNÆ NOT ELBOWED. PRONOTUM ALWAYS EXTENDING BACK TO THE TEGULÆ. TROCHANTERS 2-JOINTED. FORE-WINGS WITH A STIGMA. ABDOMEN WITH THE VENTRAL SEGMENTS MOST FREQUENTLY SOFT AND MEMBRANOUS AND WITH A FOLD. THE OVIPOSITOR ISSUING SOME DISTANCE BEFORE THE APEX OF THE ABDOMEN.

With the possible exception of the Chalcidoidea it is the largest superfamily of the order. At the present time probably less than 16,000 species have been described but undoubtedly many times this number inhabit the world. Without exception all are parasites preying upon some stage in the life-history of other insects, or occasionally upon other Arthropoda. It will, therefore, be readily appreciated that the group, as a whole, is of the greatest importance, not only on account of the rôle which it plays in the economy of nature, but also from the fact that the majority of the species are beneficial to man. For the classification of the superfamily vide Ashmead (1900).

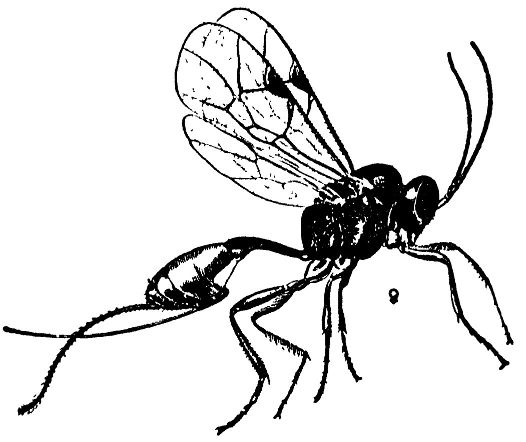

FIG 547.—*Thersilochus conotracheli*, FEMALE : ENLARGED.
After Cushman, *Journ. Agric. Res.* 6, 1916.

Table of families :

1 (8).—Winged forms.
2 (3).—Abdomen inserted upon the dorsum of the metathorax. EVANIIDÆ (p. 571)
3 (2).—Abdomen inserted normally.
4 (7).—Fore-wings with one recurrent vein or none.
5 (6).—A narrow costal cell present. STEPHANIDÆ (p. 573)
6 (5).—Costal cell obliterated. BRACONIDÆ [1] (p. 572)
7 (4).—Fore-wings with two recurrent veins. ICHNEUMONIDÆ [2] (p. 571)
8 (1).—Apterous forms.
9 (10).—All the abdominal segments flexible. BRACONIDÆ (part) (p. 572)
10 (9).—Abdominal segments not as above.
11. (12).—Abdominal segments 2 and 3 flexible. ICHNEUMONIDÆ (p. 571)
12 (11).—Abdominal segments 2 and 3 rigid and connate. BRACONIDÆ (part) (p. 572)

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[1] Except in *Lysiognatha* Ashm. which has two recurrent veins.
[2] Except in *Pharsalia* Cress. which has one recurrent vein.

FAM. EVANIIDÆ.—The members of this family are often known in America as Ensign flies from their curious habit of carrying the abdomen upraised. This region of the body is, as a rule, strongly compressed with a very slender base which is inserted on the dorsum of the metathorax. These insects are also distinguishable from all other families (except the Stephanidæ) by the presence of a distinct costal cell, the costal and sub-costal veins being clearly separated. *Evania* Ill. is an egg parasite of the Blattidæ and *E. appendigaster* L. is distributed in most parts of the world, its host being *Periplaneta*. *Gasteruption* Latr. (*Fœnus* F.) has been bred from various genera of solitary bees and wasps and its life-history has been studied by Hoppner (*All. Zeits. f. Ent.* 1904). *Aulacus* Jur. and its allies are parasitic upon Coleopterous larvæ, particularly those of the Cerambycidæ. The family has been monographed by Kieffer (*Das Tierreich, Lief.* 30, 1912), and is nearly world-wide, including about 300 species.

FAM. ICHNEUMONIDÆ (Ichneumon Flies).—The vast majority of these insects are parasites, or less frequently hyperparasites, of Lepidoptera. After the latter come the Hymenoptera, and more especially the family Tenthredinidæ, but all groups including the Parasitica may be attacked. A considerable number of Ichneumonidæ are known to utilize Coleoptera as their hosts, but Diptera are much less frequently selected. A still smaller number parasitize Arachnida, and a few attack Aphididæ and also *Hemerobius, Chrysopa* and *Raphidia*. Most species of the family are probably seldom restricted to any individual specific host, and those so accredited are becoming reduced in number with increasing knowledge. Psychologically, the Ichneumons are among the most highly evolved of all solitary insects. The remarkable instincts exhibited in the discovery of their hosts and in providing for their offspring, their mating habits, behaviour in captivity, etc., afford a wide field for investigation. The imagines are most active on warm sunny days and are partial to flowers, especially Umbelliferæ. Many species hibernate as adults but it appears to be the female, the male perishing before the advent of winter. Apterous and brachypterous forms are comparatively frequent in the sub-family Cryptinæ, and it is often a matter of difficulty to discriminate them from similarly wingless Braconidæ. In the Cryptinæ, however, the abdominal segments are soft and telescopic whereas, among the Braconidæ, the middle segments are connate and rigidly fixed. Ichneumon larvæ are composed of a variably shaped head and usually 13 body segments. Spiracles, when present, consist typically of nine pairs, which are situated on the pro- or meso-thorac, and first eight abdominal segments. Among endoparasitic larvæ, there are frequently striking differences between the earlier and later instars. One of the most characteristic features of the newly hatched larvæ of many species is the presence of a prominent caudal prolongation or tail. Owing to the fact that it disappears when the tracheal system becomes open to the exterior, this appendage has been regarded as an accessory respiratory organ, functional during the earlier stages of life. As Timberlake has remarked, there is nothing in its structure to contradict this view as it is a hollow structure lined with hypodermal cells, and is filled with blood a greater part of the time. Seurat, on the other hand, ascribes to it a locomotory function. The head in the young larva is large, and often strongly chitinized, the segments between that region and the caudal appendage are sometimes greatly compressed, and the respiratory system is apneustic. The second instar is usually of a transitional nature between the first and third. The tail, though greatly reduced, is still evident, and the head has also undergone reduction and is less strongly chitinized. In the third instar the larva generally becomes maggot-like, with a greatly abbreviated head, and the tail, as a rule, has disappeared or is vestigial. Towards the end of this stadium Timberlake states that, in *Limnerium*, the tracheal system communicates with the exterior by the spiracles. The number of instars present is obviously extremely difficult to determine: according to Cushman there are five in *Thersilochus*, and the same number is stated by Smith to be present in *Calliephialtes*. Ectophagous larvæ are always devoid of the caudal appendage, the head is well developed and chitinized, a variable growth of body hairs is evident, and the tracheal system is peripneustic from an early stage. When fully fed, Ichneumon larvæ construct silken cocoons often composed of iridescent strands of yellow, black or white threads, and in some cases the cocoon is suspended by means of a filament from the food-plant of the host. Some of the most remarkable members of the family belong to the genera *Thalessa* and *Rhyssa* whose larvæ are ectoparasites of those of the Siricidæ. The adults are notable on account of the great length of the ovipositor and for their specialized habits of egg-laying. *Thalessa* has an ovipositor which may attain a length of six inches, with which it pierces or drills the wood of trees in order to reach the burrows occupied by *Tremex*. The English *Rhyssa persuasoria* similarly parasitizes *Sirex*, and it has been recorded to reach its host by inserting the terebra along the burrows of the latter and also by passing it through the bark and solid wood. An interesting account of the habits of both genera is given by Riley (*Ins. Life* I). The familiar reddish-brown species of *Ophion,* so often attracted to lights, are common parasites of Noctuid larvæ. *Hemiteles areator* has been bred from a remarkable range of hosts comprising many Lepidoptera, various Hymenoptera including other Ichneumonidæ, and also from several Coleoptera and Diptera. *Agriotypus* Walk. is an endoparasite of trichopterous larvæ, and the adults have been observed to dive and swim beneath the water while seeking their host (vide Claasen, *Proc. Ent. Soc. Wash.* 1931). Ashmead places this genus in a family of its own on account of the hardened abdominal sterna and the spined scutellum. Among the more important life-history studies of individual species of Ichneumonidæ the reader should consult the old though important work of Ratzeburg (vol. 1, 1844), particularly for the larval development of *Anomalon* ; among others, the papers of Cushman on *Calliephialtes* (*Journ. Agric. Res.* 1) and *Thersilochus* (*Ib.* 6), Newport (1855) on *Paniscus,* Timberlake (*U. S. Bur. Ent. Tech.* Ser. 19) on *Limnerium,* and Imms (*Ann. App. Biol.* 1918) on *Pimpla* may be mentioned. Morley (1903–14) has monographed the British species, Berthoumieu (1894, etc.) those of Europe, and Schmiedeknecht (1902–11) has produced a general systematic treatise on the family.

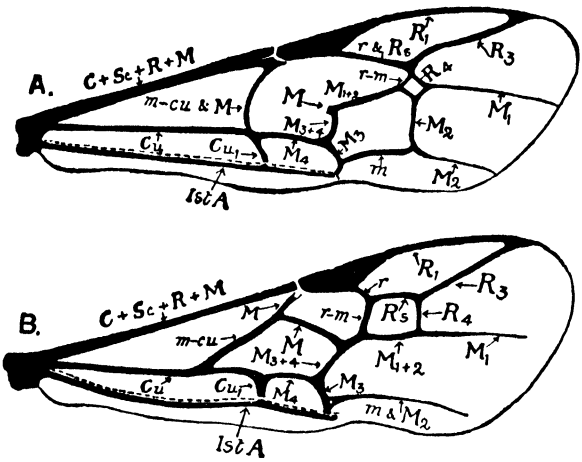

FIG. 548.—FORE-WINGS OF *A*, AN ICHNEUMON AND *B*, A BRACONID.

After Comstock, "Wings of Insects."

FAM. BRACONIDÆ (Supplementary Ichneumon Flies).—These insects are closely related in structure and habits to the Ichneumonidæ but are readily separated by 3rd discoidal and 2nd apical cells in the fore-wings being confluent. Further points of distinction are afforded by the 1st cubital and 1st discoidal cells which are usually separate, whereas in the Ichneumonidæ they are merged into one (Fig. 548). Also, with the exception of the sub-family Aphidiinæ, there is no articulation between the second and third abdominal segments. Braconidæ are easily distinguished from the Evaniidæ and Stephanidæ by the absence of the costal cell. With regard to their hosts a great variety of insects are selected ; the Lepidoptera are the most commonly parasitized, and more than one hundred examples of an individual species of Braconid may issue from a single caterpillar. Braconid larvæ are composed of thirteen body segments and, in the first instar, the head is often large and chitinized. As in the preceding family, the most frequent number of spiracles in the adult larva is nine pairs, of which the first is placed as a rule on the mesothorax, and the remainder on the first eight abdominal segments. The endoparasitic forms are often provided with a caudal appendage similar to that found in Ichneumonid larvæ. In *Apanteles, Microplitis, Microgaster,* and probably in other closely allied genera, this appendage is wanting, and the proctodæum is evaginated to form a swollen anal vesicle, which has been regarded as an accessory respiratory organ. Weissenberg (*Sitz. Ges. Natur. Freunde Berlin,* 1908), from the analogy of the hind-gut of other parasitic larvæ, considers its most important function to be that of excretion. Pupation may occur within the host as in *Rhogas* and *Aphidius* or, more usually, externally as in *Apanteles* and many other genera. The pupa is enclosed in a cocoon which, in the last-named genus, is composed of fine threads of white, yellow, or buff-coloured silk. In *Microgaster* the cocoon is of a glistening papyraceous nature. Very frequently members of a species emerging from the same host construct their cocoons in a mass, often enveloped by a common web. They may be closely compacted to form a cake, the individual cocoons being regularly arranged so as to resemble honeycomb. The biology of *Apanteles* has been studied by many observers, notably Grandori (1911), Seurat (1899), Muesebeck (1918) and others. It is a common endoparasite of lepidopterous larvæ, *A. glomeratus* being an abundant enemy of *Pieris,* a single larva of which may support nearly 150 examples. When mature the larval parasites gnaw their way through the skin of the host, and construct sulphur-yellow cocoons, irregularly heaped together. The biology of *Microgaster* is very similar and *M. connexus* is a common parasite of *Porthesia similis* (Gatenby, 1919). The species of *Alysia* and their allies are distinguished by the peculiar attachment of the mandibles, the apices of the latter being directed outwards and not meeting when closed. Those Braconids which exhibit this curious feature are separated by Ashmead into a distinct family—the Alysiidæ. Almost all their species are parasitic upon dipterous larvæ and the biology of *Alysia manducator* Panz has been followed by Altson (*Proc. Zool. Soc.* 1920). It is a common endoparasite of *Calliphora, Lucilia* and other Muscids; the young larva has a caudal appendage, and becomes maggot-like with nine pairs of open spiracles in the last instar. One of the most remarkable Braconids is *Sycosoter lavagnei* which is an ectoparasite of the Scolytid *Hypoborus ficus* (vide Lichtenstein and Picard, 1918): both sexes are dimorphic, having winged and apterous forms, but in the male the alate forms are the commoner.

The Aphidiinæ are parasites of Aphididæ, more especially of the apterous viviparous females and, as a general rule, only a single larval parasite develops within the body of an individual host. The life-history of *Aphidius testaceipes*, which is a common enemy of *Toxoptera graminum*, has been followed by Webster and Phillips (*U.S. Bur. Ent. Bull.* 110). These observers state that the aphid may be attacked in any of its instars but if parasitized before the second ecdysis the host fails to reach to maturity. On the other hand, if the *Aphidius* deposits its egg in an aphid which has passed the second ecdysis the parasitism does not prevent its attaining the adult stage. If the aphid has passed the third ecdysis before becoming parasitized, it is capable in all cases of producing a small number of young before succumbing. When about to pupate the *Aphidius* larva makes a ventral fissure in the body-wall of its host, and cements the latter down to the object upon which it finally rests. The dead parasitized aphids are familiar straw-coloured objects and each bears a circular hole through which the adult parasite issued. Species of *Praon* leave their host prior to pupation and construct for themselves a separate shelter, which is usually surmounted by the empty body of its victim (Fig. 549). The British species of Braconidæ have been monographed by Marshall (1885–99), and Lyle has contributed notes on their biology (*Entom.* 1914 et seq.).

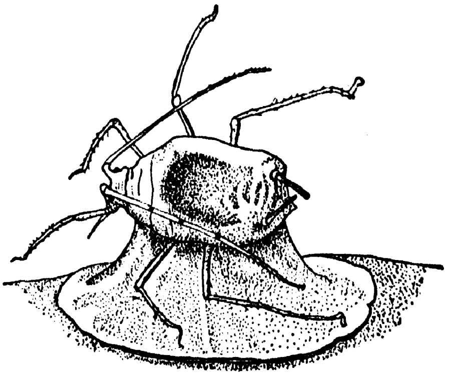

FIG. 549.—COCOON OF *PRAON* BENEATH THE BODY OF ITS DEAD HOST (AN APHID).

After Howard.

FAM. STEPHANIDÆ.—The members of this small family have very slender antennæ composed of 30 or more joints and the abdomen and the ovipositor are likewise elongate. The antennæ are situated far forwards near to the clypeus, the hind femora are usually swollen and spined beneath, and the hind-wings are most frequently without basal cells. About 100 species have been described (vide Elliot, *Proc. Zool. Soc.* 1922) and they appear to be parasites of wood-boring insects.

Superfamily **Chalcidoidea** (Fig. 550)

ANTENNÆ ELBOWED. PRONOTUM NOT EXTENDING BACK TO THE TEGULÆ. TROCHANTERS 2-JOINTED. FORE-WINGS WITHOUT A STIGMA OR CLOSED CELLS. ABDOMINAL STERNA HARD AND CHITINIZED WITHOUT A FOLD: OVIPOSITOR ISSUING SOME DISTANCE BEFORE THE ANAL EXTREMITY.

The superfamily is probably the largest in the order as regards number of species and it also includes some of the smallest members of the Insecta. The bulk of its species are either parasites or hyperparasites of other insects, and are of even greater economic importance than those of the Ichneumonoidea as a natural means of control. Non-parasitic vegetable-feeding forms are comprised in the families Agaonidæ, Torymidæ and Eurytomidæ: in the majority of cases they infest seeds but certain members of the last-mentioned family are gall-producers on various Gramineæ. The parasitic species, in a relatively small number of instances, are indirectly injurious from the fact that they destroy beneficial insects such as *Tachardia lacca*, or are hyperparasites of other insects which, in their turn, are destroyers of harmful species. The orders most commonly parasitized are the Lepidoptera, Hemiptera-Homoptera and Diptera. Lepidoptera are more frequently selected than any other major group, enormous numbers of their eggs and larvæ succumbing to infestation by various Chalcids: on the other hand their pupæ are rarely affected. Certain Pteromalidæ, however, prefer to oviposit in larvæ just about to pupate or in newly transformed pupæ. The Coccidæ are the most universally attacked of any family of insects, and some species (*Coccus capreæ*, etc.) are so freely infested that it is often rare to find an immune individual. In temperate regions Chalcids seem to pass through from one to three generations in the year—a higher number is apparently rare. One of the shortest life-cycles occurs in *Euplectrus comstockii*, which develops from the egg to the adult in seven days (Schwarz, *Am. Nat.* 1881), and an equally rapid development is found in *Trichogramma pretiosa*, which has been reared from the eggs of *Aletia xylina* (Hubbard). Chalcid larvæ are composed, as a rule, of a reduced head and thirteen trunk segments. In the ectophagous forms open spiracles are evident at the time of hatching: thus in *Aphelinus mytilaspidis* the full number of eight pairs are present at this stage. In other cases, as in *Torymus propinquus*, a reduced number of spiracles is present at the time of eclosion from the egg, additional pairs being acquired subsequently. Among endophagous species the younger larvæ are usually apneustic, open spiracles developing later when the destruction of their hosts reaches an advanced stage. In *Blastothrix* and other genera the newly hatched larva is exceptional in being metapneustic (Fig. 551). This condition is an adaptation which allows of the respiration of atmospheric air through the pedicel of the egg, which protrudes externally through the body-wall of the host and functions as a kind of respiratory tube. In *Blastophaga psenes* the tracheal system is apneustic throughout life (Grandi). Hypermetamorphosis is common in the superfamily, and at least five types of primary larvæ are known, but probably others await discovery. In the later instars all these types assume an ovoid maggot-like form and, in the majority of

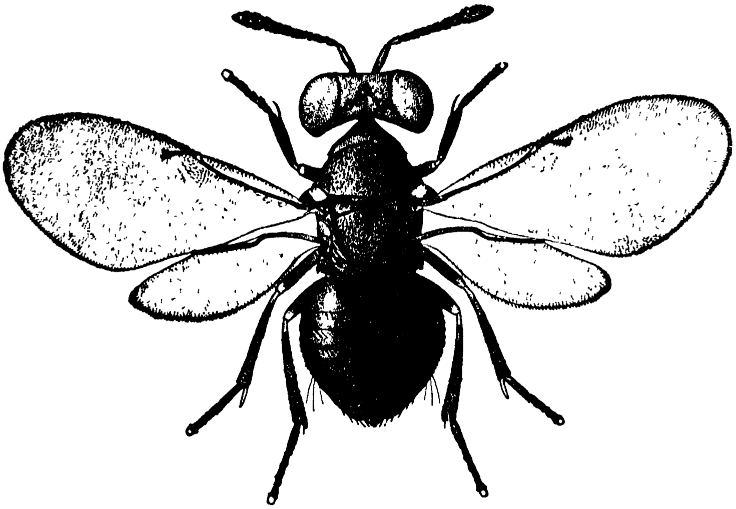

FIG. 550.—A TYPICAL CHALCID, *BLASTOTHRIX SERICEA*, FEMALE: MAGNIFIED.

species, the latter kind of larva is retained throughout life. Chalcid larvæ do not construct any cocoons (except in *Euplectrus*, see p. 578), and pupation usually occurs either within or in close proximity to the remains of their hosts.

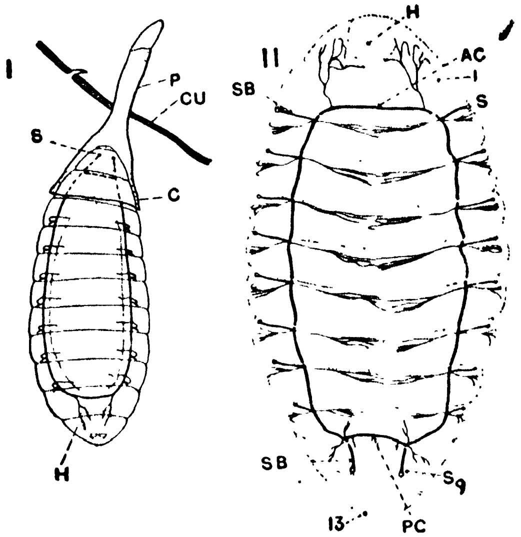

FIG. 551.—*BLASTOTHRIX SERICEA.* I, NEWLY-HATCHED LARVA RESPIRING THROUGH THE PEDICEL (*P*) OF THE EGG.

C, remains of chorion ; *CU*, body-wall of host ; *H*, head ; *S*, spiracles.

II, LARVA IN LAST INSTAR.

AC, *PC*, anterior and posterior tracheal commissures ; 1, 13, 1st and 13th trunk segments. S_1, S_9, 1st and 9th spiracles ; *SB*, spiracular tracheæ.

For the classification of the Chalcidoidea and keys to the major divisions and genera vide Ashmead (1904) : a general account of the biology of the group is given by Parker (1924). Life-history studies of individual species are numerous ; in Europe a series of papers has been contributed by Silvestri (*Boll. Lab. Zool. Portici*) and a large number by other authors will be found in various American journals and bulletins. Some of the more important of these papers are referred to under the families concerned. A monograph on the British species is greatly to be desired and over 1,400 species are listed by Morley (1910).

Key to the families :

1. Thorax greatly elevated, scutellum much enlarged and produced behind apex in a bizarre manner. EUCHARIDÆ (p. 577)
2. Wings nearly veinless, with very long fringes : hind pair linear, very narrow and stalked at the base. Antennæ without ring-joints, scape short. Ovipositor issuing near apex of abdomen. MYMARIDÆ (p. 579)
3. Females with head oblong, marked with a broad longitudinal dorsal furrow. Fore- and hind-legs very stout, middle pair short or aborted, ovipositor long and prominent. Males apterous, with short 3–9 jointed antennæ. Abdomen broadly sessile, long and tubular. AGAONIDÆ (p. 576)
4. Not as in 1, 2 or 3.
5 (20).—Tarsi generally 5-jointed, anterior tibial spur large : axillæ with anterior margin straight and not produced in front of tegulæ.
6 (7).—Middle legs long, with large stout tibial spurs : mesopleura without a femoral furrow. ENCYRTIDÆ (p. 578)
7 (6).—Spurs of middle tibiæ short or weak : mesopleura with a femoral furrow.
8 (9).—Hind tibiæ with one apical spur : ovipositor rarely long : mandibles stout with 3 or 4 apical teeth. PTEROMALIDÆ (p. 578)
9 (8).—Hind tibiæ with two apical spurs.
10 (13).—Hind coxæ very large and long.
11 (12).—Hind coxæ sharply ridged above, triangular in section : hind femora rarely inflated. Ovipositor usually long. TORYMIDÆ (p. 577)
12 (11).—Hind coxæ more or less cylindrical : hind femora much swollen and toothed or denticulate ventrally. Hind tibiæ arcuate, the tarsi inserted just before the apex. CHALCIDIDÆ (p. 577)

13 (10).—Hind coxæ not conspicuously large.
14 (17).—Pronotum large and quadrate or not narrower than the mesonotum.
15 (16).—Abdomen rounded or ovate: 2nd tergum never very large: mandibles commonly 4-dentate. EURYTOMIDÆ (p. 577)
16 (15).—Abdomen small, triangular, mostly formed by the 2nd and 3rd terga: mandibles 2–3 dentate. PERILAMPIDÆ (p. 577)
17 (14).—Pronotum narrower in front or transverse, rarely as wide as the mesonotum.
18 (19).—Mesepisternum small: femora never much dilated. MISCOGASTERIDÆ (p. 579)
19 (18).—Mesepisternum large: either the anterior, posterior, or both femora much dilated. CLEONYMIDÆ (p. 579)
20 (5).—Tarsi 3- to 5-jointed: axillæ produced forward level with or in advance of the tegulæ: tibial spurs small or weak.
21 (22).—Tarsi 4- to 5-jointed: fore-wings not short and broad, pubescence normal EULOPHIDÆ (p. 578)
22 (21).—Tarsi 3-jointed: fore-wings short and broad, pubescence usually arranged in lines. TRICHOGRAMMIDÆ (p. 578)

FAM. AGAONIDÆ (Fig insects).—A family which includes some of the most remarkable of all Chalcids both as regards their structure and biology. Sexual dimorphism has reached a very highly specialized condition, the males being wingless and greatly modified in other respects, bearing no resemblance to the members of the opposite sex. The species are caprifiers that live within the receptacles and pollinate, or fructify, the flowers of various species of *Ficus*. The number of known species and varieties of fig is said to reach five hundred and, in certain of these, the caprification phenomena are known to vary widely, and many of the insects involved are apparently confined to certain definite species of figs. The investigation of the symbiotic relationship between plant and insect offers, therefore, an extremely wide field for investigation. The best known species is *Blastophaga psenes* L., which exists in a state of symbiosis within the fruit of *Ficus carica*. It is well known that, in the Smyrna variety of fig, the receptacles contain only female flowers, and pollination is brought about by the agency of this Chalcid. On the other hand, the caprifigs, or varieties which contain male flowers, are the natural hosts of the *Blastophaga*. Caprification, or the process of hanging caprifigs in the Smyrna trees, is an old custom based upon the belief that the figs would not mature unless it were carried out. Much discussion has arisen with reference to whether caprification is essential or not. In California it is agreed that the culture of the Smyrna fig necessitates the simultaneous cultivation of caprifying varieties in which the *Blastophaga* lives. If the latter insect fails to pollinate the Smyrna figs, the fruit falls without maturing. The eggs of this Chalcid are laid in the ovaries of the caprifig and give rise to galls therein. The male imago emerges first and, on finding a gall containing a female, commences to gnaw a hole through the wall of the ovary and fertilizes the female while the latter is still *in situ* (Fig. 552). The female leaves the receptacle through the opening at its apex and, laden with adherent pollen, flies to a neighbouring fruit. If the latter be in the right condition she seeks the opening and gains admission into the interior of the receptacle, where she commences oviposition. Should the caprifig, from which she has emerged, be suspended in a tree of the Smyrna variety she enters a fruit of the latter, but subsequently discovers that she has selected a wrong host, as the flowers are of such a shape that they do not allow of oviposition within them. After wandering about for a while, she usually crawls out of the receptacle and incidentally pollinates the flowers. The males mostly die without ever leaving the receptacles in which their development took place.

According to Baker (1913) the active caprifier and normal inhabitant of the receptacles of *Ficus nota* in the Philippines is *Blastophaga nota* Bak., and related to the latter species is a complex Chalcid association. *Agaonella larvalis* and *Sycophaga* are probably inquilines, and *Sycoryctes philippensis*, along with other Chalcids parasitizes the *Blastophaga*. In India Cunningham (*Ann. Bot. Gard. Calcutta* I) states that the complete development of *Ficus roxburghii* is dependent upon the access of the fig-insects to the interior of the receptacles and, should their entry fail to occur, both male and female flowers abort. Grandi (1920) has investigated the structure and biology of *Blastophaga psenes* and gives a full bibliography. The taxonomic writings of the latter author (*Boll. Lab. Zool. Portici* 1916 et seq.) also deal with the external morphology of many genera. Papers by Mayr, Saunders, and Grandi should also be consulted.

FAM. TORYMIDÆ.—A very large family whose affinities lie more closely with the Agaonidæ than any other group. Members of the sub-family Idarninæ are found associated with fig-insects either as parasites or inquilines. Their males are often apterous, but the abdomen is short and not tubularly lengthened or broadened at the apex as in the Agaonidæ. The great majority of Torymidæ are parasites of gallicolous insects, but a certain number have been reared from the nests of bees and wasps. Species of *Megastigmus* have been bred from hymenopterous and dipterous gall-makers while others are phytophagous, attacking the seeds of Coniferæ, *Rosa*, etc. *Syntomaspis druparum* Boh. is the apple-seed Chalcid of Europe and North America. *Monodontomerus* Westw. parasitizes many insects, *M. obsoletus* F. having been bred from both Lepidoptera and Hymenoptera. *Podagrion* Spin. is quite exceptional in being a parasite of the eggs of Mantidæ, and *Torymus propinquus* Fœrst. is an ectoparasite of gall-forming Cecidomyids (vide Seurat 1899).

FAM. CHALCIDIDÆ.—This group according to Ashmead attains its maximum development in S. America and is rather poorly represented elsewhere : eight species are listed by Morley as being British. Many of its members are primary or secondary parasites of lepidopterous larvæ or pupæ ; *Chalcis* Spin. has also been reared from larvæ of *Stratiomyia* and *Leucospis* F. from various genera of bees and wasps. The biology of *L. gigas* has been observed by Fabre (1886) : it undergoes hypermetamorphosis and is an ectoparasite of *Chalicodoma muraria.*

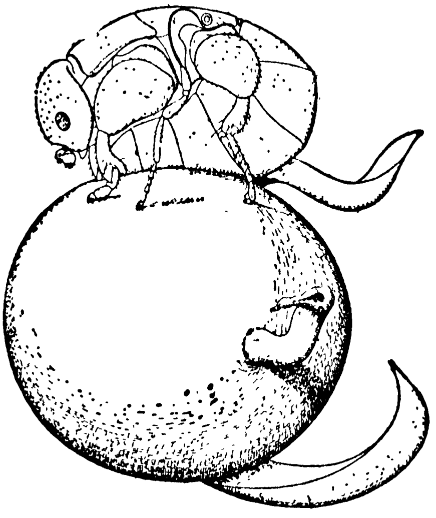

FIG. 552.—MALE *BLASTOPHAGA PSENES* FERTILIZING THE FEMALE, THE LATTER WITHIN A GALLED FLOWER OF THE FIG. *After* Grandi, *Boll. Lab. Zool. Portici* 14, 1929.

FAM. EURYTOMIDÆ.—Probably no other family of Chalcids exhibits so wide a diversity of habits as is met with among the members of this group. *Harmolita* (*Isosoma*) produces galls on the stems of wheat, rye, barley and various grasses (vide Phillips, *U.S. Dep. Agric. Bull.* 808). *H. grandis* Riley exhibits alternation of generations : the apterous form, *minutum*, occurs in spring, laying its eggs at the base of the young wheat plant, and the larva destroys the tiller affected, or may kill the entire plant. The alate form, *grandis*, is the summer generation which lays its eggs slightly above the nodes. Males are rare and have only been found in the case of the spring brood : *H. orchidearum* Westw. is exceptional in that it produces galls on the stems and leaves of certain orchids (*Cattleya*). *Bruchophagus funebris* How. is likewise phytophagous and passes its developmental stages in the seeds of clover and alfalfa. Species of *Eurytoma* and other genera attack the seeds of plum, grape, Ampelopsis, etc. Other members of the family live in the nests of bees and wasps or are parasites of gall-forming Diptera and Hymenoptera ; a few are egg-parasites of Orthoptera, while several species of *Eurytoma* appear almost ubiquitous in their selection of hosts.

FAM. PERILAMPIDÆ.—A small family distinguishable from the preceding by the large thorax and small triangular abdomen. The biology of *Perilampus hyalinus* Say, a hyperparasite of the larva of *Hyphantria* and other hosts, has been studied by Smith (*Bur. Ent., Tech. Ser.*, 19, pt. 4 : *Psyche*, 1917). The newly hatched larva is an active planidium which bores its way into the *Hyphantria*, in whose body-cavity it remains until it meets with either the larva of the Tachinid *Varichæta* or of the Ichneumon *Limnerium*, which are primary parasites. Upon discovering one or other of the latter hosts it becomes endoparasitic : subsequently it makes its way out, undergoes hypermetamorphosis into a white maggot-like larva and becomes an ectoparasite of the same host.

FAM. EUCHARIDÆ.—Included herewith are certain remarkable metallic blue or green Chalcids characterized by the configuration of the scutellum which is frequently produced backwards in the form of powerful spines. So far as known they are ectoparasites of ants and are mainly found in the tropics. *Orasema* Cam. attacks members of the genera *Pheidole* and *Solenopsis.* According to Wheeler (1907) it parasitizes the prepupa just after the last exuviæ have been stripped off by the worker ants. Its newly hatched larva is a planidium and is found attached near to the head of the host. As a result of the parasitism the hosts undergo degeneration and fail to become imagines. For the biology of *Schizaspidia* see Clausen, *Ann. Ent. Soc. Am.* 16.

FAM. ENCYRTIDÆ.—The Chalcids comprised in this extensive family live as parasites of the ova, larvæ, or pupæ of various insects. Although the Hemiptera-Homoptera and Lepidoptera are most frequently selected hardly a single order of insects is immune from their attacks. Certain genera are definitely restricted with reference to their selection of hosts. Thus *Aphycus* is an ecto- or endo-parasite of Coccidæ, particularly of *Coccus* L.; *Blastothrix* almost exclusively parasitizes *Coccus* and *Pulvinaria* while *Ageniaspis* is mainly confined to the lepidopterous genera *Lithocolletis* and *Hyponomeuta.* On the other hand *Eupelmus* affects a wide range of species, having been reared from the eggs of Saturnidæ and other of the larger Lepidoptera, from the puparium of *Glossina,* and from Cecidomyidæ, Coccidæ and various Coleoptera. The family is of more than ordinary interest and important from the fact that certain species of *Ageniaspis* (*Encyrtus*), *Litomastix* and *Copidosoma,* which parasitize Lepidoptera, are known to exhibit polyembryony. They deposit their eggs in those of the hosts but the larvæ of the latter emerge in the normal manner and contain the developing parasites in their body-cavity where embryonic fission takes place (vide p. 165). Several members of the family have been the subject of detailed biological studies and reference should be made to papers on *Ageniaspis* by Bugnion (1891) and Marchal (1904), on *Encyrtus* (*Comys*) by Embleton (1904), on *Aphycus* and *Blastothrix* by Imms (1918), on *Copidosoma* by Leiby (1923) and *Litomastix* by Silvestri (1906). The work of Mercet (*Mus. Nat. Cien. Madrid,* 1921) on the Spanish species is well illustrated and is a valuable taxonomic monograph.

FAM. PTEROMALIDÆ.—This family is the largest among Chalcids and its members, like those of the Encyrtidæ, affect almost all orders of insects either as parasites or hyperparasites. *Pteromalus puparum* is one of the commonest of all Chalcids and is widely distributed: it especially parasitizes *Pieris rapæ* and *brassicæ* and an account of its biology is given by Martelli (1907). *P. deplanatus* Nees has been recorded as occurring in great swarms in buildings but there is no satisfactory explanation of the habit (vide Scott, *Ent. Month. Mag.* 1919). *Nasonia brevicornis* Ashm. is a common pupal parasite of *Musca domestica, Calliphora* and other Calypteræ (vide Altson *Proc. Zool. Soc.* 1920). *Spalangia muscidarum* is likewise a pupal parasite of *Musca, Stomoxys,* and *Hæmatobia,* its larva undergoing hypermetamorphosis (Richardson 1913). *Isocratus* and *Pachyneuron* parasitize aphides, etc., and the Eunotinæ mainly affect Coccidæ, *Scutellista cyanea* Motsh. being an important factor in the control of the Black Scale (*Saissetia oleæ*) in California and of *Ceroplastes rusci* in Italy.

FAM. EULOPHIDÆ.—A very large family consisting for the most part of very small species. The Aphelinini are important parasites of the Diaspine coccids and of aphids, their larvæ being either ectophagous or endophagous. *Aphelinus mytilaspidis* de B. is a common ectoparasite of the Mussel Scale and its structure and biology has been fully studied (Imms, 1916). *Prospaltella berlesei* Silv. has been introduced into Italy for the purpose of controlling *Diaspis pentagona* and there is now a voluminous literature on the subject. The Tetrastichini affect nearly all orders of insects either as primary or secondary parasites: the majority parasitize gallicolous Diptera, Hymenoptera, and Coleoptera. *Tetrastichus asparagi* Cwfd. is an egg-parasite of *Crioceris asparagi* and, according to Johnston (*Journ. Ag. Res.* 4, 1915), from 1 to 10 larvæ occur in a single egg. The beetle larvæ emerge from the infested eggs but fail to pupate, although a pupal cell is constructed, and the adult parasites issue from the latter. *Melittobia* Westw. (*Anthophorabia* Newp.) is a common ectoparasite of the pupæ of *Bombus, Osmia,* and other *Aculeata* (vide Balfour-Browne, *Parasitology* 1922) as well as of certain Diptera, more especially *Calliphora.* Members of the sub-family Eulophinæ are principally primary or secondary parasites of leaf-mining Lepidoptera. *Euplectrus* is exceptional in that a cocoon is present. Thomsen (*Vidensk. fra Dansk naturh. Foren.* 84, 1927) has shown that it is constructed from the products of the Malpighian tubes which are modified in the hind-gut and discharged through the anus.

FAM. TRICHOGRAMMIDÆ.—The 3-jointed tarsi separate this family from all others and, according to Ashmead, it is related to the Eulophidæ, connecting the latter with the Mymaridæ. Over 100 species are known, all are egg-parasites, and they include some of the most minute examples of the Insecta. *Trichogramma* usually parasitizes Lepidoptera and Howard mentions that as many as 20 individuals will develop within a single egg. In Europe *T. evanescens* is a parasite of *Donacia* and certain Odonata (vide Gatenby 1917) and of many Lepidoptera. *T. minutum*, in America, has been extensively used in connection with biological control. *Prestwichia aquatica* Lubb. has been reared from the eggs of *Notonecta*, *Ranatra*, *Dytiscus* and *Pelobius*, while *Hydrophylax aquivolans* parasitizes those of *Ischnura*. The last-named Chalcid swims beneath the water by the aid of its wings. *Poropœa stollwercki* Forst. affects the eggs of *Atellabus* and, according to Silvestri, it passes through five larval forms.

FAM. MYMARIDÆ (Fairy Flies).—The species of this family are all exceedingly minute and, similarly to those of the preceding group, they are exclusively egg-parasites. They are mostly black or yellowish and devoid of metallic colours. Most authorities place them among the Proctotrypoidea but Ashmead regards their position to be in the present superfamily. One of the most remarkable genera is *Polynema* which parasitizes Hemiptera : *P. natans* utilizes *Notonecta* as its host and both sexes swim readily beneath the water by means of their wings. *Alaptus* Hal. includes probably the smallest of all insects, *A. magnanimus* Ann. measuring only ·21 mm. in length. *Anaphes conotracheli* Gir. has been reared from the eggs of weevils and *Litus Krygeri* Kieff. from those of *Ocypus olens.*

In addition to the preceding there are several other families of lesser importance. The **MISCOGASTERIDÆ** are allied to the Pteromalidæ and, according to Ashmead, the only reliable character to separate them is the number of apical spines on the hind tibiæ. Very little information exists as to their biology but they have been reared from a variety of hosts. The **CLEONYMIDÆ** are nearest related to the Encyrtidæ and the European forms have been mainly reared from colopterous hosts. The Brazilian *Pelecinella* Westw. includes some of the largest and most striking of all Chalcids. The **ELASMIDÆ** are a small family resembling the Eulophidæ on account of their 4-jointed tarsi but their inflated hind coxæ and the compressed femora serve to separate them. They are mostly minute black species infesting lepidopterous larvæ.

Superfamily **Cynipoidea**

ANTENNÆ NOT ELBOWED. PRONOTUM EXTENDING BACK TO THE TEGULÆ. TROCHANTERS USUALLY 1-JOINTED. FORE-WINGS WITHOUT A STIGMA, WITH FEW CLOSED CELLS AND REDUCED VENATION. ABDOMINAL STERNA HARD AND CHITINIZED WITHOUT A FOLD : OVIPOSITOR ISSUING SOME DISTANCE BEFORE THE ANAL EXTREMITY.

Included in this superfamily are about 1,200 species of small, and often minute, insects which are usually black or darkly coloured. Biologically, they are of great interest as the various species are either gall-makers, inquilines or parasites, the first-mentioned exhibiting the phenomena of heterogeny and agamogenesis. The eggs are provided with a usually elongate pedicel, the larvæ are apodous and maggot-like, and there is no cocoon. In the great majority of the imagines the second abdominal tergum is larger than the remainder and in many cases forms almost the whole of the dorsal surface of the abdomen. The trochanters are described by most authors as being 2-jointed but, as Kieffer points out, the apparent second joint is formed by the contracted base of the femur. Authorities differ with regard to the division of the group into families; five principal families are dealt with in the pages which follow. The leading work on the group is that of Kieffer (1879, etc.) which forms part of the great treatise of André. The former author (1914) has also written an admirable shorter account, which is accompanied by a full bibliography ; Morley's synopsis (*Entom.* 1931–32) and Cameron's monograph (1882–92) refer to the British species. For a catalogue of the world's species vide Dalla Torre and Kieffer (1910).

FAM. CYNIPIDÆ (Gall Wasps and Inquilines).—VENTRAL SURFACE OF ABDOMEN NOT, OR ONLY PARTLY, HIDDEN BY OVERLAPPING TERGA, 2ND TERGUM VERY LARGE :

SCUTELLUM SCULPTURED. The greater number of its members belong to the subfamily Cynipinæ, all of which produce galls for the purpose of providing shelter and nutriment for their offspring. Their larvæ are consequently internal feeders and are maggot-like in form, with well chitinized dentate mandibles. The head is small and is followed by twelve body segments, and there are nine pairs of spiracles. The antennæ and both pairs of palpi are vestigial. Pupation takes place within the larval cell and a cocoon is wanting. The forms of galls produced by these insects are almost endless and all parts of plants may be affected, from the roots to the flowers. In every case the female insect lays an egg or eggs in the tissues of the growing plant, in the interior of which the subsequent development takes place. As a rule this mode of life is accompanied by the production of a gall. Many theories have been advanced to account for the phenomena of gall-formation, but the problem appears to be still far from being solved, largely on account of difficulties attending the experimental side of the subject. A full discussion of the various views which are or have been held is given in the works of Kieffer. The irritation of the tissues produced by the insertion of the ovipositor is not the initial cause. There also appears to be no evidence that the fluid injected by the female during oviposition is anything more than of the nature of a lubricant. The mere presence of the Cynipid egg in the tissues is not in itself sufficient to produce the gall as, ordinarily, the latter does not commence to develop until the larva has hatched; many months may elapse between the date of oviposition and that of eclosion. All that can be said is that the galls are produced as the result of reactions of the cambium and other meristematic tissues of the plant in response to the stimulus induced by the presence of the living larva. It is probable also that the latter exudes a secretion which exercises an influence upon the growth of the cells of the plant (vide Triggerson 1914). The formation and structure of the galls have been studied by Beyerinck (1882), Cook (1902–04), Cosens (1912) and others. Viewed in section, a gall is usually seen to be composed of the following layers of tissue passing from without inwards (Fig. 553). The outermost coat is the epidermis and beneath the latter is an extensive development of parenchymatous tissue. The third layer is protective in function and is usually of a hard consistency but is sometimes wanting, while the innermost layer is nutritive and surrounds the cell containing the larva. Cook concludes that the morphology of a gall is dependent, as a rule, upon the insect which produces it rather than upon the plant upon which it is produced. Galls formed by the same genus of insects exhibit great similarity even though produced on widely different plants. Furthermore, those produced on a particular genus of plants by different insects are very dissimilar. In addition to the species which actually forms the gall, the latter frequently supports a definite biological association of other insects. A large number are inquilines, which comprise not only other Cynipidæ but also larvæ of Diptera, Coleoptera and Lepidoptera. Furthermore, the larvæ and pupæ of the true gall-maker, and of the inquilines, are very subject to the attacks of hymenopterous parasites, more particularly Chalcids. Kinsey (1920) estimates that 86 per cent. of the known species of gall-wasps produce galls on *Quercus* and are confined to that genus. Another 7 per cent. are restricted to species of *Rosa* and the remaining 7 per cent. are found on plants belonging to 35 genera of Angiosperms, more especially the Compositæ. The reason for this very marked selection of a single genus of plants is hard to understand, particularly as oaks have a limited distribution in the present age. It is true that the galls on this genus are more conspicuous than on other plants where they are more liable to become overlooked. According to Kinsey the tribe Aulacini is, in many respects, the most primitive of the gall-wasps. Its members are not confined to a particular plant host but select those belonging to many genera. Not only are they more or less polyphagous as a group, but certain of the species utilize several genera of plants, *Aulacidea tumida* for example, selecting *Solidago, Sonchus* and *Lactuca*. The various species of *Aulacidea* either induce extremely simple gall-formation or live in stems, producing no gall at

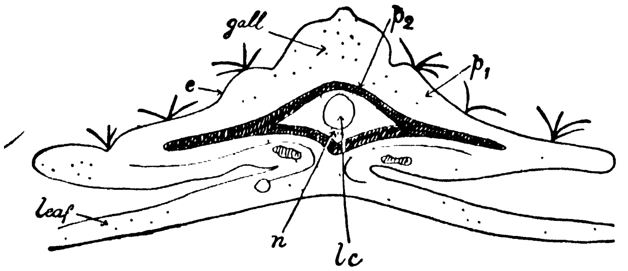

FIG. 553 —DIAGRAMMATIC SECTION OF GALL OF *NEUROTERUS LENTICULARIS*, ACCORDING TO FOCKEU.

e, epidermis; p_1, parenchyma; p_2, protective layer; *n*, nutritive layer; *lc*, larval cell.

all. They have not acquired agamic reproduction, the sexes are produced in about equal numbers, and the alternation of generations so characteristic of the higher Cynipinæ is absent. Almost every transition may be observed from the simple condition prevalent in *Aulacidea* to the many types of highly complex galls, and the alternation of morphologically and physiologically different generations found in many other genera. The most highly evolved galls are to be looked upon as almost entirely separate organisms, which are only connected to the host plant by means of a narrow neck of tissue. In some cases the galls develop in size and form new tissue after separation from the parent plant. The galls of two successive generations, produced on different parts of the same plant, often present entirely different forms; and the insects of the two generations are frequently so divergent in characters that they have often been allocated to separate genera until their relationships have been detected. Heterogeny among Cynipidæ is of an exceptionally remarkable nature. In many species males have never been seen at all, out of many thousands of the insects which have been reared, and there appears to be little doubt of their non-existence. In these very highly specialized cases the successive generations are all similar and agamic and a secondary simplification of the life-cycle results. The majority of the Cynipinæ have only the alternate generations alike: each agamic generation is followed by a bisexual generation which, in its turn, produces the agamic one. The latter is the overwintering stage while the bisexual generation is produced during summer. A few of the commoner species, which are prevalent in Britain, may be selected as illustrating the principal biological phenomena already referred to. *Neuroterus lenticularis* is a very abundant gall wasp in England. The galls from which the spring (agamic) generation emerges are lenticular growths found on the lower surface of oak leaves in October. The insects remain in the galls all the winter, and appear as adults early in April. They consist entirely of parthenogenetic females which deposit their eggs deep down among the catkins and young leaves. The resulting galls occur in May and June and are quite different from those preceding, being spherical and sappy in character. The summer generation which emerges from them was originally referred to a different insect, i.e. *Spathegaster baccarum*. Both males and females are produced but the latter largely predominate in numbers. After copulation the eggs are laid at the sides of the veins in the tissues of the young leaves, and the resulting galls are of the lenticular kind found in October. The most conspicuous difference in the females of the two generations is seen in the ovipositor, which is much larger in the agamic than in the summer individuals. *Biorrhiza pallida* Oliv. is another very characteristic oak species. In the bisexual generation the males are winged, and the females are either apterous or have vestigial wings. This generation emerges from the "oak apple" galls and the eggs are laid in the roots of that tree. In this situation other galls are produced from which, in spring, the agamic generation (known as *B. aptera* Bosc.) is produced. The individuals of this brood consist exclusively of apterous females which migrate up the tree and produce the "oak apple" galls in due course. The genus *Rhodites* is confined to the Rosaceæ—*Rosa* and *Rubus* being most usually selected. The familiar and striking bedeguar or "pin-cushion" galls are produced on the former genus by *Rhodites rosæ*. These galls consist of a mass of moss-like filaments surrounding a cluster of hard cells containing the *Rhodites* larvæ. There is no alternation of generations in this species, males are much less frequent than females, and the eggs are known to be capable of parthenogenetic development. The hard spherical "marble" galls of *Cynips kollari* on the oak produce the agamic generation of that species. This insect was apparently introduced into England about 1830 and is now abundant. According to Beyerinck the bisexual generation is the insect known as *Andricus circulans* Mayr.

The Synerginæ are almost entirely inquilines, and are often mistaken for true gall-makers to which they frequently bear an extremely close resemblance. They mostly lay their eggs in cynipid galls found on oak, but have also been reared from galls formed by Diptera and other insects.

FAM. IBALIIDÆ.—FOUR BASAL SEGMENTS OF ABDOMEN SUB-EQUAL IN BOTH SEXES: 2ND JOINT OF HIND TARSI WITH A LONG PROCESS: PRONOTUM BASALLY ELEVATED. The members of this small family are among the largest Cynipoidea. The genus *Ibalia* is widely distributed in Europe and N. America and its members are endoparasites of Siricidæ. The single British species *I. leucospoides* has been studied in great detail by Chrystal (*Oxford Forest. Mem.* 11, 1930). The egg is laid in the *Sirex* larva and the 1st instar larva is of the polypod type with 12 pairs of trunk limbs: the whole larval period appears to last three years.

FAM. CHARIPIDÆ (Allotriidæ).—BODY, INCLUDING SCUTELLUM, SMOOTH AND IMPUNCTATE: 2ND ABDOMINAL TERGUM LONGER THAN THE REST TOGETHER. The members of this family are mainly hyperparasites of aphides through *Aphidius* or other parasites: less frequently they have similar relations with coccids. An account of the biology of *Charips* is given by Haviland (*Quart. Journ. Mic. Sci.* 65, 1921).

FAM. EUCOILIDÆ (Fig. 554).—SCUTELLUM RUGOSE OR PUNCTATE WITH A RAISED CUP-LIKE DEPRESSION IN THE CENTRE: 2ND ABDOMINAL TERGUM USUALLY HALF THE LENGTH OF THE ABDOMEN AND GENERALLY WITH A BASAL HAIR FRINGE. These insects are parasites of Diptera and the primary larvæ are eucoiliform. In *Kleidotoma* the 2nd instar larva is polypod with 10 pairs of trunk limbs (James, *Ann. App. Biol.* 15, 1928). *Eucoila eucera* is an important parasite of *Oscinella frit* and *Cothonaspis rapæ* attacks *Chortophila brassicæ.*

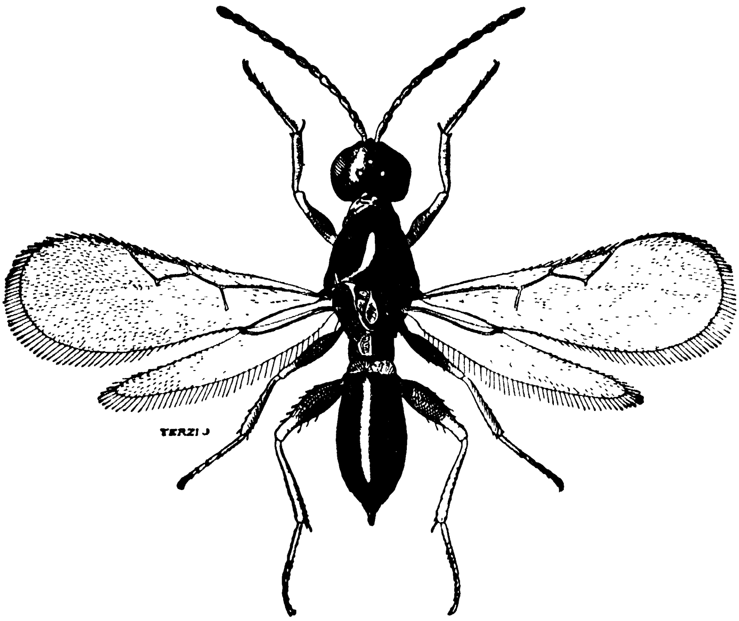

Fig. 554.—*Eucoila eucera*, Female. Britain.

FAM. FIGITIDÆ—SCUTELLUM SCULPTURED BUT WITHOUT CUP-LIKE RAISED DEPRESSION: 2ND ABDOMINAL TERGUM LESS THAN HALF THE LENGTH OF ABDOMEN. The species of *Figites* and other genera are parasites of Diptera while *Anacharis* has been bred from *Hemerobius*. The primary larva of *Figites* is eucoiliform and is followed by a polypod instar with 10 pairs of trunk limbs (vide James, *loc. cit.*). The Anacharitinæ and Aspiscerinæ are sometimes regarded as separate families.

Three other families of Cynipoidea are extra-European.

Superfamily **Proctotrypoidea (Serphoidea, Oxyura)**

PRONOTUM EXTENDING BACK TO THE TEGULÆ, TROCHANTERS 2-JOINTED (EXCEPT IN PELECINIDÆ). OVIPOSITOR ISSUING FROM THE APEX OF THE ABDOMEN, ITS OUTER SHEATHS CONJOINED TO FORM A MORE OR LESS CYLINDRICAL TUBE.

The members of this superfamily are slender insects mostly of small size and nearly all are parasites. Many attack the eggs of other insects, other species are endoparasites of larvæ or pupæ, some are hyperparasites and a small number are inquilines. The majority of species form a cocoon of a silky or parchment-like nature but in the aphid-infesting genera the pupa is protected by the body of the host. The wings exhibit the greatest diversity of venation and in many forms they are almost veinless, while apterous species are very frequent. For a general account of the group vide Ashmead (1893) who, in his later work (1902–03), revised its classification. By some authorities these insects are considered to be closely allied to the Chalcids but according to Ashmead they are in every respect more intimately related to the Vespoidea. The British species have scarcely been investigated, but a standard work on the European forms by Kieffer (*Das Tierreich, Lief.* 41, 42, 44) is available.

Tables of families:

A. WINGED FORMS

1 (2).—Trochanters 1-jointed. PELECINIDÆ (p. 583)
2 (1).—Trochanters 2-jointed.
3 (10).—Antennæ inserted on the middle of the face, often on a frontal protuberance.
4 (7).—Fore-wings with a more or less distinct stigma.
5 (6).—Mandibles dentate: antennæ 14 or 15-jointed, hind-wings with distinct venation. HELORIDÆ (p. 583)
6 (5).—Mandibles edentate: antennæ 13-jointed with one ring joint: hind-wings without distinct venation. PROCTOTRYPIDÆ (p. 583)
7 (4).—Fore-wings without a distinct stigma.
8 (9).—Hind-wings with a basal cell: antennæ 14 to 15-jointed, labial palpi 3-jointed. BELYTIDÆ (p. 583)
9 (8).—Hind-wings without a basal cell: antennæ 11 to 14-jointed, labial palpi 2-jointed. DIAPRIIDÆ (p. 584)
10 (3).—Antennæ inserted at the junction of the clypeus and face.
11 (12).—Abdomen never acute or margined along the sides: antennæ 10 or 11-jointed. CERAPHRIONIDÆ (p. 585)
12 (11).—Sides of abdomen acute or margined.
13 (14).—Antennæ usually 12-jointed, sometimes 7- or 11-jointed in female: fore-wings generally with marginal and stigmal veins. SCELIONIDÆ (p. 584)
14 (13).—Antennæ not more than 10-jointed: fore-wings usually veinless. PLATYGASTERIDÆ (p. 585)

B. WINGLESS FORMS

1 (6).—Antennæ inserted on the middle of the face, often on a frontal protuberance.
2 (3).—Mandibles edentate: apex of abdomen stylate. PROCTOTRYPIDÆ (p. 583)
3 (2).—Mandibles dentate: apex of abdomen non-stylate.
4 (5).—Labial palpi 3-jointed. BELYTIDÆ (p. 583)
5 (4).—Labial palpi 2-jointed. DIAPRIIDÆ (p. 584)
6 (1).—Antennæ inserted at the junction of the clypeus and face.
7 (8).—Abdomen never acute or margined along the sides. CERAPHRIONIDÆ (p. 585)
8 (7).—Sides of abdomen acute or margined.
9 (10).—Antennæ 12-jointed or, if clavate, 7-jointed: labial palpi 2-jointed. SCELIONIDÆ (p. 584)
10 (9).—Antennæ usually 10-jointed: labial palpi 1-jointed. PLATYGASTERIDÆ (p. 585)

The **PELECINIDÆ** occur in N. and S. America and are in many ways an exceptional family. In the female the abdomen is greatly attenuated and measures about five times the length of the head and thorax, while in the male the abdomen is short and clavate. *Pelecinus polyturator* Dr. is tolerably common in the temperate parts of N. America where it has been recorded as a parasite of the larvæ of *Lachnosterna*: its females attain a length of 50 to 60 mm. The **HELORIDÆ** are a small but widely distributed family known to parasitize Chrysopidæ. The **PROCTOTRYPIDÆ** may be recognized by the long tubular sheath to the ovipositor and, in the male, the abdomen is terminated by a pair of spine-like processes. Their larvæ appear to be mainly parasitic upon those of Coleoptera; and an account of the biology of *Phænoserphus* is given by Eastham in *Parasitology*, vol. 21, 1929. The **BELYTIDÆ** are known to parasitize fungivorous dipterous larvæ and *Belyta fulva* Cam. has been recorded from *Bolitophila luminosa*. The **DIAPRIIDÆ** are also known to parasitize dipterous larvæ, and the biology of *Diapria conica*, which attacks *Eristalis tenax*, has been followed by Sanders (*Can. Ent.*, 1911). The **SCELIONIDÆ** are a very large and widely distributed family and its species are egg-parasites of other insects (mainly Orthoptera and Hemiptera) or, in a few cases, of spiders. The biology of *Teleas* has been studied by Ganin (1869) and Ayers (1884) and that of *Eumicrosoma* by McColloch (*Journ. Econ. Ent.*, 1915) : the former attacks the eggs of *Œcanthus* and the latter parasitizes those of *Blissus leucopterus*. In *Riela manticida* Kieff, an exceptionally advanced type of parasitism is presented (vide Chopard, *Ann. Soc. Ent. Fr.*, 91). Its development takes place in the eggs of *Mantis religiosa* and the adult parasites make their way to the imagines of the host upon whose bodies they settle down. In this situation they cast off their wings and lead an ectoparasitic life. Where the mantis is a female, and has commenced oviposition, the *Rielia* migrates to the genital region in order to lay its eggs in the viscid mass of the ootheca while the latter is being formed. Parasites which settle upon male mantids are short-lived and perish along with their hosts. The **CERAPHRIONIDÆ** are known to parasitize Cecidomyidæ and Aphididæ, but it appears to be uncertain in many cases whether they are parasites or hyperparasites. The biology of *Lygocerus* has been followed by Haviland (*Q.J.M.S.*, 1920), the species observed being ectoparasites of the larvæ and pupæ of *Aphidius* which lives as an internal parasite of various aphides. There appear to be four larval instars and the primary larva is ovoid, with a reduced head and no tail-like appendage. Only two pairs of spiracles are present and these are placed between the first and second segments and on the fourth segment respectively : at a later stage seven pairs of spiracles are present. The **PLATYGASTERIDÆ** (Fig. 555) form the largest family of Proctotrypoidea and its species mainly parasitize Cecidomyidæ (vide Mar-

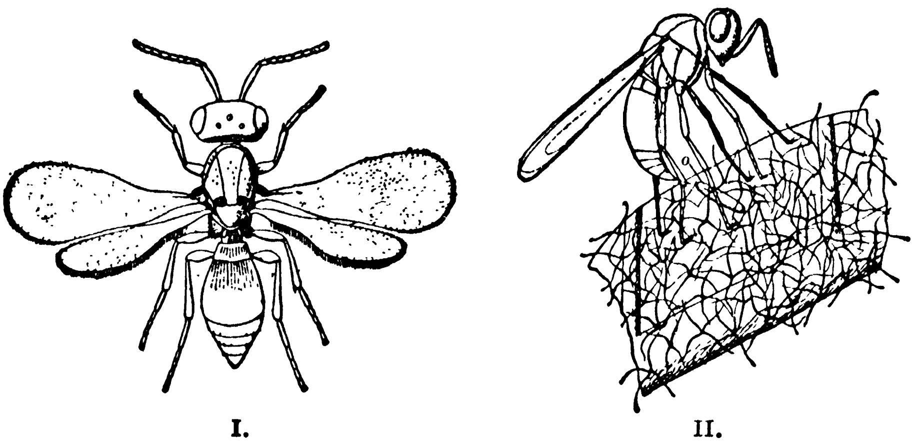

FIG. 555.—I, *Platygaster dryomiæ*, Female ; II, The same in the act of Oviposition in an Egg O, of *Dryomyia* (Cecidomyidæ) on a Leaf.

After Silvestri, *Boll. Lab. Zool. Portici* 11, 1921.

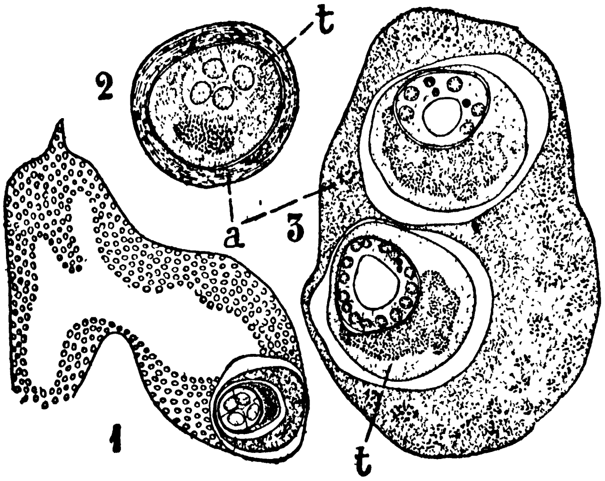

FIG. 556.—*Platygaster dryomiæ*. 1, Embryo in Morula Stage in the Brain of Larva of *Dryomyia* (sagittal section). 2, An Embryo with Trophamnion *t* and adventitious Layer *a*. 3, Two Embryos in the Blastula Stage enclosed in a common adventitious layer.

After Silvestri, *loc. cit.*

chal, 1906). Their eggs are usually laid within those of their host, but the development of the latter is not arrested since the larval parasite does not develop until after the eclosion of the larval Cecidomyid. The localization of these parasitic larvæ within their hosts is variable. Thus, *Synopeas rhanis* lives free in the body-cavity of the larva of *Perrisia ulmariæ* : *Platygaster minutus* lives in the stomach of *Mayetiola destructor* while *Trichacis remulus* forms cysts in the ventral nerve cord of that same host. On the other hand, larvæ of *Platygaster dryomiæ* (Fig. 556) and *Inostemma piricola* live in cysts in the brain of their hosts. The females of the last-mentioned genus possess a long horn-like growth on the 1st abdominal segment which curves forwards over the thorax. This peculiar projection is a special adaptation for lodging the elongate ovipositor, and the latter instrument is used for piercing the blossom-buds of the pear in order to insert the eggs within those of the host (*Contarinia pirivora*).

Superfamily **Formicoidea (Heterogyna : Ants)**

SOCIAL AND POLYMORPHIC INSECTS WITH GENICULATE ANTENNÆ. PRONOTUM EXTENDING BACK TO THE TEGULÆ BUT THE LATTER ARE EITHER ABSENT OR IMPERFECT IN THE WINGLESS FORMS. TROCHANTERS 1-JOINTED. PETIOLE WITH ONE OR TWO SCALES OR NODES.

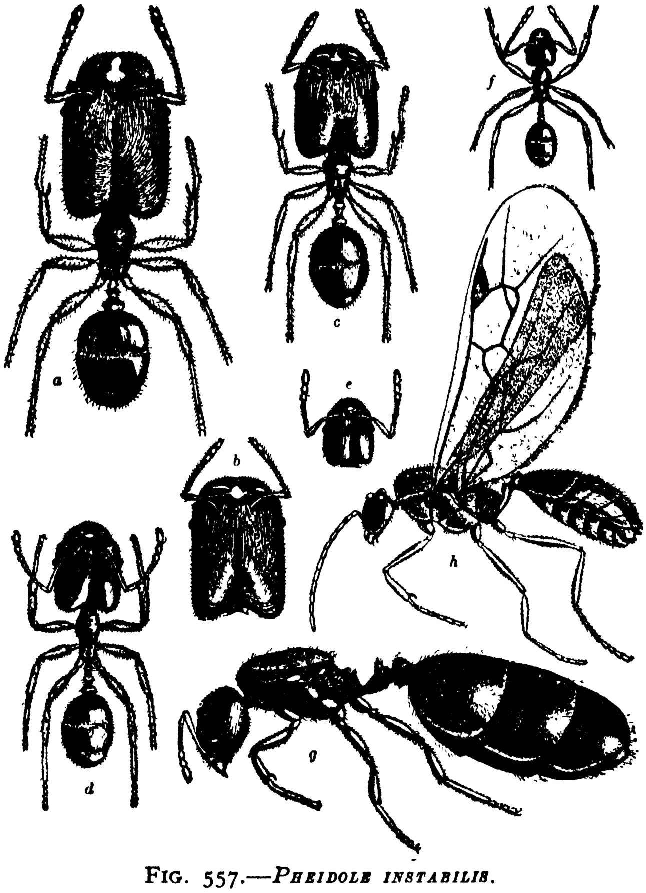

FIG. 557.—*Pheidole instabilis.*

a, Soldier; *b–e*, intermediate workers; *f*, typical worker (micrergate); *g*, deälated female; *h*, male. *After* Wheeler, " Ants."

The ants constitute a single very large family—the Formicidæ which embraces, according to Wheeler, about 3,500 described species. They are all social and, with the exception of a few parasitic forms, have a well-differentiated worker caste (Fig. 557). The demarcation between the head, thorax and abdomen is highly accentuated ; the latter region, furthermore, is sharply differentiated into a narrow basal region or *pedicel*, formed by the apparent first or first and second segments, and a globular or ovoid *gaster* formed by the remaining seven or eight segments.

The head varies enormously in shape, and the mandibles present an almost bewildering variety of form, and are subjected to many uses. The labrum is vestigial, the maxillæ are composed of the usual sclerites, and their palpi are 1 to 6-jointed. The laciniæ are membranous and toothless, thereby indicating a liquid diet. In the labium both submentum and mentum are evident, together with a median glossa : at the base of the latter is a pair of small paraglossæ beset with rows of setæ. The labial palpi are 1 to 4-jointed. The antennæ are composed of 4 to 13 joints and usually the male has one more joint than the female or worker. Compound eyes and three ocelli are well developed in the males, but in the females, and especially the workers, the eyes are usually reduced or vestigial. The abdomen is the seat of a stridulating organ which consists of an area of extremely fine parallel striæ on the mid-dorsal integument of the base of the gaster (Fig. 103). The sharp edge of the preceding segment overlaps this area, and is deflexed, so that it may scrape backwards and forwards when the segments are moved on each other, thereby producing a highly pitched sound. A large and well developed sting is present in the females and workers of the sub-families Ponerinæ, Dorylinæ and most Mymecinæ, but is vestigial or absent in the remainder.

Ants, as Wheeler observes, have acquired an extensive and uniform experience with all developmental stages of their progeny which they not only feed and clean, but also transport from place to place as conditions may demand. The eggs are small, hardly more than ·5 mm. long even in the largest species, and the popular expression of "ants' eggs" is erroneously applied to the cocoons or even to the larvæ or pupæ. The larva consists of a head and 13 trunk segments: eyes are wanting and in a few cases vestigial antennæ are present. There are ten pairs of spiracles, situated on the meso- and meta-thorax and the first eight abdominal segments. The body is almost always invested with hairs which assume many forms and are most abundant in the first instar. In many genera of the Ponerinæ there are girdles of large segmentally repeated tubercles. Different species adopt very different methods of nourishing their larvæ. Many feed them only on regurgitated liquid while carnivorous species give them portions of other insects, the harvesting ants utilize fragments of seeds, and the fungus growers nourish their larvæ with fungus-hyphæ. Wheeler states that a cocoon is constantly present in the most primitive ants and equally constantly absent in large groups of highly specialized forms.

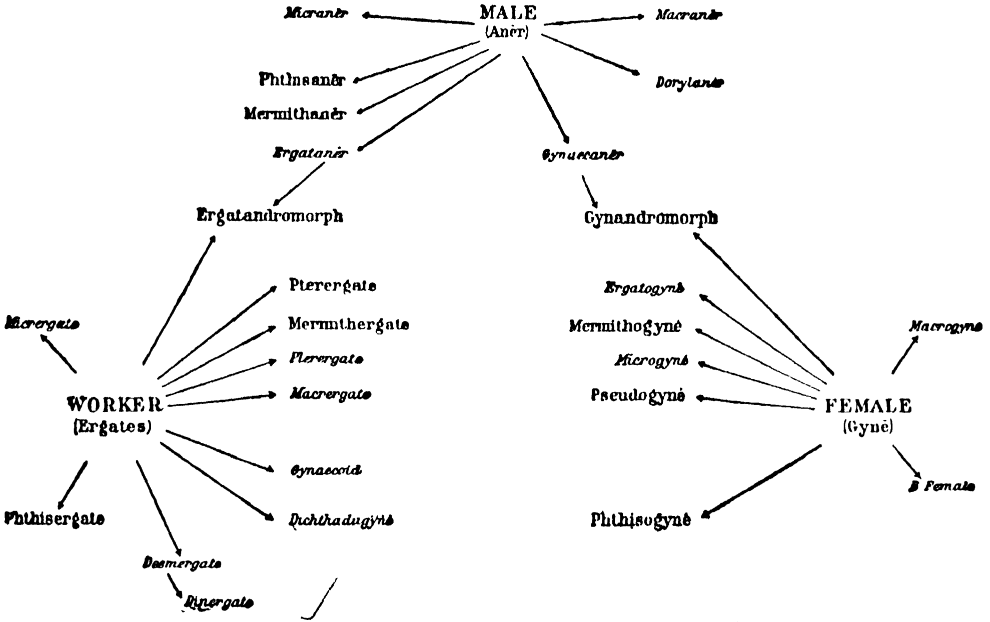

FIG. 558.—DIAGRAM OF POLYMORPHISM AMONG ANTS.

Adapted from Wheeler, "Ants."

Polymorphism attains its highest expression among ants and no less than 29 distinct types of morphologically different individuals have been recognized. The various phases among ants may be divided into the normal and the pathological and, in the accompanying diagram (Fig. 558), the latter are represented in italics. The normal phases may be subdivided into primary or typical and secondary or atypical. The normal phases comprise only the original male, female and worker, while the atypical phases form the remainder. It will be observed that in the diagram the three typical phases are at the angles of an isosceles triangle ; excess developments are placed to the right side and defect developments to the left, of a vertical line passing through the middle of the diagram. The arrows indicate the directions of the affinities of the secondary phases and suggest that those on the sides of the triangle are annectant, whereas those which radiate outward from its angles represent new departures with excess and defect characters. The pathological phases are in italics.

A. The *male* (*anēr*) is the most stable of the three typical castes. The sense organs, wings and genitalia are highly developed but the mandibles are imperfectly so. The head is proportionately shorter, smaller and rounder than in females and workers of the same species, and the antennæ longer and more slender.

B. The *female* (*gynē*) or queen is characterized by her large stature and well developed reproductive organs. She is usually longer than the male and worker of the same species and attains a great size in certain exotic forms. The antennæ and legs are often shorter and stouter than in the male, the mandibles are well developed and the gaster large.

C. The *worker* (*ergate*) is characterized by the absence of wings and the reduced thorax and small gaster. The eyes are small and the ocelli either absent or minute. A receptaculum seminis is usually wanting and the ovarioles are greatly diminished in number. The antennæ, mandibles, and legs are well developed. In many species the workers are of various sizes ; in others they are dimorphic, there being no intermediate forms.

D. When a member of any of the above castes assumes an unusually large size it is known as a *macraner*, *macrogyne* or *macrergate* according to whether it is a male, female, or worker.

E. A dwarf form of these castes is termed a *micraner*, *microgyne* or *micrergate* as the case may be.

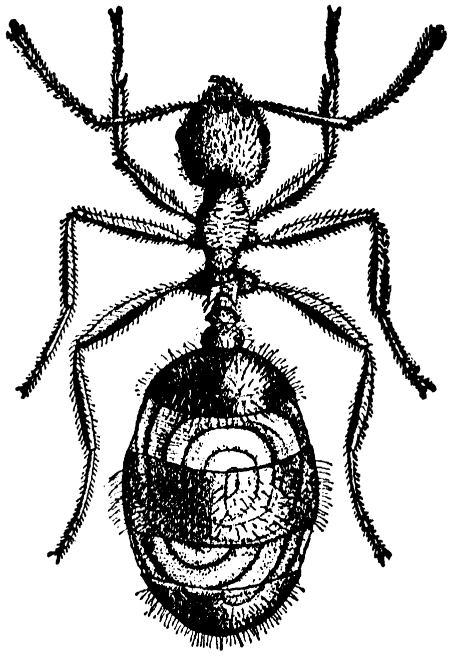

FIG. 559.—MERMITHERGATE OF *PHEIDOLE COMMUTATA*.

After Wheeler.

F. Individuals of certain tropical ants are sometimes parasitized in the larval or prepupal stage by *Orasema* (p. 577). They fail to attain the imago stage ; wings, if normally present, are suppressed, and many parts remain abortive. Such an individual is termed a *phthisaner*, *phthisogyne* or *phthisergate* according to its caste.

G. Similarly, individuals may be parasitized by the Nematode *Mermis*. The effect of this parasitism is to produce a shortening of the wings in the male or female : in the worker the body becomes enlarged and has a tendency to exhibit female characters as regards the thorax and ocelli (Fig. 559). An individual supporting this worm is termed a *mermithaner*, *mermithogyne* or *mermithergate*.

H. The males and females sometimes resemble the worker and are devoid of wings. In the case of the males they may possess only the same number of joints to the antennæ as the worker. In some species the sexes are dimorphic, the normal individuals coexisting with the modified apterous forms. An individual of the latter type is designated an *ergataner* or *ergatogyne* according to its sex.

I. An unusually large form of the male occurs in the Dorylinæ and is termed a *dorylaner*. It is characterized by the large and peculiar mandibles, the long cylindrical abdomen and the singular genitalia. It may be regarded as an aberrant macraner that has become the typical male form in this sub-family.

J. The *gynæcaner* is a male which resembles the female rather than the male, and has the same number of antennal joints as the former sex. This phase occurs in the parasitic workerless genera *Anergates* and *Epœcus*.

K. The *gynandromorph* is an anomalous individual in which the male and female characters are combined either laterally or in a more or less mosaic manner. An *ergatandromorph* is a similar anomaly but has the worker instead of the female characters combined with those of the male.

L. The *β-female* is an aberrant female characterized by the excessive developments of the antennæ and legs and in the pilosity of the body. If it coexists with the normal female the latter is then termed the *α*-female.

M. An apterous worker-like individual which combines the size and gaster of the worker with the thoracic characters of the female is termed a *pseudogyne*.

N. The *gynæcoid* is an egg-laying worker and is a physiological rather than a morphological phase, as it is probable that all worker ants if abundantly fed become capable of oviposition. Should a colony lose its queen one or more workers may become egg-laying substitution queens as has been found by Donisthorpe in several species of British ants. In a few cases the queen phase has disappeared and is replaced by the gynæcoid worker. The *dichthadiigyne* is peculiar to the Dorylinæ and is probably a further development of the gynæcoid. It is without eyes, ocelli or wings and the gaster and ovaries are exceedingly voluminous.

O. The *dinergate* or *soldier* is recognized by the large head and mandibles which are often adapted to particular functions such as fighting, guarding the nest, crushing seeds and other hard food particles, etc.

P. The *desmergate* is a form intermediate between the ordinary worker and the dinergate.

Q. The *plerergate* or *replete* is a worker which has acquired the peculiar habit of distending the gaster with stored liquid food until it becomes a spherical sac often so large as to interfere with locomotion.

R. The *pterergate* is a worker or dinergate with vestigial wings, the thorax remaining unmodified.

When both sexes are winged mating nearly always takes place during what is termed the nuptial flight. As a rule one or other sex predominates in any particular colony and, since the nuptial flight for the colonies of a particular species in the same neighbourhood takes place synchronously, means is thus afforded for intercrossing with individuals of different colonies. Prior to the marriage flight, the workers become much excited and direct the operation, preventing the males and females from leaving the nest until the right time. There is good reason to believe that meteorological conditions exercise an important influence in this matter. There exist in literature many references to great nuptial swarms of ants which sometimes cloud the air like smoke. On descending to earth the impregnated female divests herself of her wings, and the deälated individual commences to excavate a small chamber, within which she remains in seclusion until her eggs are mature, and ready to be laid. During the whole of this period, which may extend for months, the chamber is sealed up, and the female draws entirely upon the nutriment afforded by her fat-body and degenerating flight muscles. When the first larvæ appear, they are fed by the secretion of her salivary glands until they pupate. As soon as the workers are mature they break through the soil and establish a communication between the brood chamber and the outer world. They then go abroad and forage for food, and share it with their exhausted parent. The latter is now relieved from the care of the brood, and she limits her activities to egg laying, imbibing liquid food directly from the mouths of the attendant workers. In this capacity, she lives on solely for the purpose of egg-production, sometimes to an age of fifteen years. The number of ants in a fully developed colony appears to vary between wide limits. Yung has made actual counts in the case of *Formica rufa* and found that the numbers vary between about 19,900 and 93,700 ; in *Formica pratensis* Forel estimated that the largest mound may contain as many as 500,000 individuals, a figure which Yung regards as excessive.

The nests or formicaries present an almost bewildering variety of architecture. Not only has every species its own plan of construction, but this plan may be modified in various ways in adaptation to special local conditions. The Dorylinæ can hardly be stated to construct nests, and usually have their abode in some available recess beneath a stone, or log, or they may even temporarily occupy nests of other ants. A large number of ants construct nests in the soil and these habitations consist of a number of more or less irregular excavations, either with or without a definite superstructure around the entrances. The excavations are divided into galleries, or passages of communication, and chambers leading off from the latter. The chambers are used as nurseries for the brood, as granaries for storing seeds, as fungus gardens and for other purposes. In some species there is nothing to indicate the situation of a subterranean nest, the excavated soil being carried some distance away and scattered irregularly. In others it is heaped up in the vicinity of the entrance, or entrances, to the nests, to form a crater, which varies in size and construction among different ants. Such craters are often difficult to distinguish from mound or hill nests. The latter are usually much larger and are formed not only of excavated soil but also of straws, twigs, pine-needles, leaves, etc., and are perforated with galleries and chambers. Such mound nests are well exhibited in the European *Formica fusca.* Perhaps the largest number of ants' nests are excavated beneath stones or logs. In the tropics many ants take advantage of cavities found in stems, petioles, thorns and bulbs, or even in the spaces enclosed by the overlapping leaves of certain epiphytes. Cavities in the bark, the dead wood, and stumps of trees are also frequently utilized, and even old deserted Cynipid galls. Suspended nests are of frequent occurrence, hanging from trees in tropical and subtropical forests. These are constructed of earth, carton, or silk and contain anastomozing galleries and chambers. *Œcophylla smaragdina* forms leaf nests, the leaves being fastened together by means of a silken web. The observations of Doflein and others have proved that the silk is provided by the larvæ of the species concerned. They are held by the workers in their jaws and used, as it were, as shuttles in weaving the silken tissue of the nest.

Of the seven [1] sub-families into which the Formicidæ are divided the most primitive are the Ponerinæ (Fig. 560). They are characteristic of the tropics and are the dominant group of ants in Australia. The only genus found in Britain is *Ponera* which is represented by two species, and in *P. punctatissima* Rog. the males are ergatoid. The nests of the Ponerinæ are subterranean and are usually only occupied by a few dozen individuals. The three castes differ very little in size ; the workers are monomorphic, they feed their larvæ with portions of other insects, and the pupæ are enclosed in cocoons. The "bull-dog" ants (*Myrmecia*) of Australia attain a length of 2–2·5 cm. and, as Wheeler remarks, they bite and sting with such ferocity that few observers care to study them at close quarters.

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[1] For the characters of these sub-families vide Wheeler (1922): the classification of ants has been somewhat modified since the one given in that author's text-book (1910).

The Dorylinæ include the driver and legionary ants of the tropics; they are likewise carnivorous, but the workers are blind and highly polymorphic, varying from large soldiers with toothed mandibles, though intermediates, to micrergates. The females (dichthadiigynes) are very little known and seldom found: they are very large, blind, and wingless like the workers, and have relatively enormous abdomens. The males (dorylaners) are likewise very large, with sickle-shaped mandibles, and peculiar genitalia. These insects do not construct permanent nests but merely bivouac in temporary quarters, and wander from place to place in long files. Their sorties are only made on sunless days or at night and are for predatory and migratory purposes. Belt mentions columns of *Eciton* which he followed for two or three hundred yards without coming to the end. Their prey consists of insects and spiders of various kinds, but Savage records that *Anomma* will succeed in killing large animals if the latter be penned up, and he mentions having lost monkeys, pigs and birds by these insects.

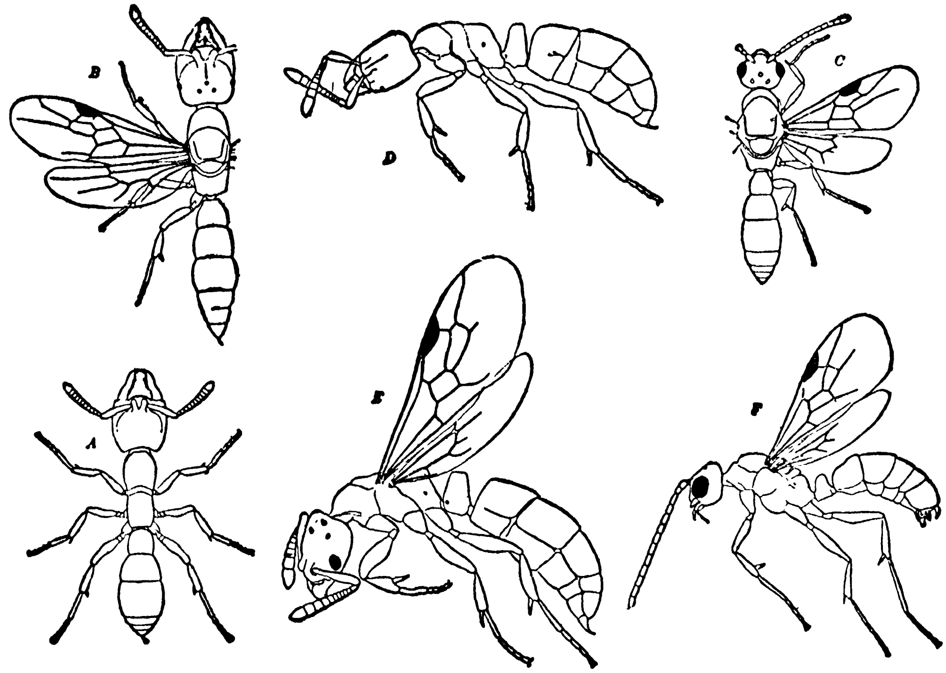
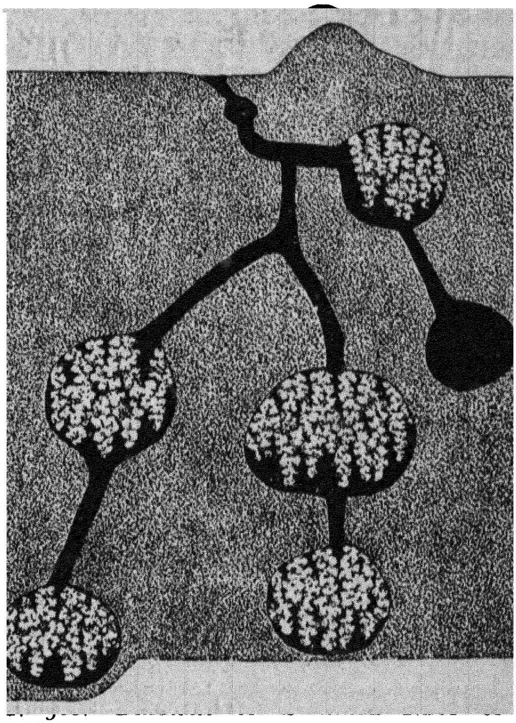


FIG. 560.—PONERINE ANTS. A, B, AND C, WORKER, FEMALE AND MALE OF *STIGMATOMMA PALLIPES*; D, E, F, WORKER, FEMALE AND MALE OF *PONERA PENNSYLVANICA*.

After Wheeler, "Ants."

The Ponerinæ, Dorylinæ, together with the small sub-family Cerepachyinæ and many of the lower Myrmecinæ are carnivorous ants which represent the savage or hunting stage in the evolution of those insects. The remaining groups of ants have largely abandoned this habit and adopted a vegetarian diet. Wheeler has called attention to the fact that an abundance of food is necessary for the maintenance and fullest development of social life. In warm arid countries insect food is either very scarce, or competition to secure it very keen among ants and other animals. A number of the former have become vegetarians as their last resource in the struggle for existence. Under such circumstances, the seeds of herbaceous plants provide an accessible nutritious food, and the outcome of this is the harvesting habit which is prevalent in many species. The four higher sub-families, however, have an extremely varied diet, since they not only imbibe the secretions of nectaries, the honey-dew or products of Aphides and other Homoptera, but also feed upon fungi, fruit, seeds and other substances. The harvesting habit appears to have arisen sporadically, and often in distantly related genera, but all of which pertain to the sub-family Myrmecinæ. In species of *Messor*, for example, the ants have been observed to gather the seeds both from the ground and from the plants, remove their envelopes, and cast the chaff and empty capsules on the kitchen middens outside the nest. In confirmation of Pliny and Plutarch, Moggridge mentions that the ants bite off the radicle to prevent germination. The latter process is also arrested by the ants bringing the seeds when damp to the surface, spreading them in the sun, and then carrying them back to the special chambers or granaries wherein they are stored.



Trachymyrmex septentrionalis showing, near Surface, small Original Chamber of Queen, Chambers with pendent Fungus Gardens and newly excavated Chamber.

After Wheeler, " Ants."

The Myrmecine tribe of the Attini, which is peculiar to tropical and sub-tropical America, are all fungus-growers and fungus-eaters, and number about 100 species. The fungi are cultivated in special chambers of the nest termed fungus-gardens (Fig. 561) and, according to Moeller (1893), these gardens are practically pure cultures of the fungi concerned, being assiduously " weeded " and tended by the ants. Neither free aerial hyphæ, nor any form of fruit body develop, but whether this is due to their elimination by the ants, or to environmental conditions, is uncertain. A fungus-garden is a sponge-like mass of comminuted eaf-fragments or, in some cases, of insect excrement. The fungi grow rapidly on this substratum and produce numerous swellings or bromatia. The latter form he food of the ants and their arvæ and have never been produced in cultures. The systematic position of these fungi is unettled : several genera have been described which have been reerred to the Ascomycetes and Basidiomycetes. The formation of a new ungus-garden is undertaken by the queen who, before departing for the mating flight, fills her infra-buccal pocket (p. 556) with fungal hyphæ. This pellet is expelled within the newly made nest-chamber and the growing hyphæ are nourished, at first, by the fæces of the insect, who may even sacrifice some of her eggs for the same purposes.

The small tropical sub-family Pseudomyrminæ is notable for its highly pecialized larvæ. The head in these larvæ is surrounded by the hood-like horax and lies far back on the ventral surface, where it is in contact with the first abdominal segment. The latter somite bears a pocket, or trophothylax, and food received from the workers is deposited in this pouch, from which it s gradually drawn into the mouth and swallowed. As previously mentioned

(p. 545) trophallaxis is highly developed, the larvæ supplying their nurses with the secretions of their remarkable exudatoria.

Ants have become associated with a large number of phytophagous insects which possess the habit of excreting liquid of a kind which is exceedingly palatable. In return, the ants render many of such insects certain services, and the relations thus established may be regarded as a kind of symbiosis. The insects most concerned belong to various families of the Homoptera, viz. Aphididæ, Coccidæ, Membracidæ, Psyllidæ, etc., together with the larvæ of the Lycænidæ. In the case of many Aphididæ and Coccidæ, for example, they are afforded protection by the ants, who construct tents or shelters for housing them. With Aphidæ the ants frequently betray their sense of ownership by at once carrying them away to safety should the nest be disturbed. This solicitude on the part of the ants may extend to the eggs of the aphids also, and numerous observers have noted ants collecting and storing Aphid eggs in autumn and tending the nymphs when they emerge. The latter are carried and placed upon stems or roots which may be situated either within the nest or at some distance outside the latter. Nearly 70 species, representing 29 genera, of Lycænidæ are mentioned as having larvæ that are attended by ants, and the relationship in some cases may be exceedingly intimate.

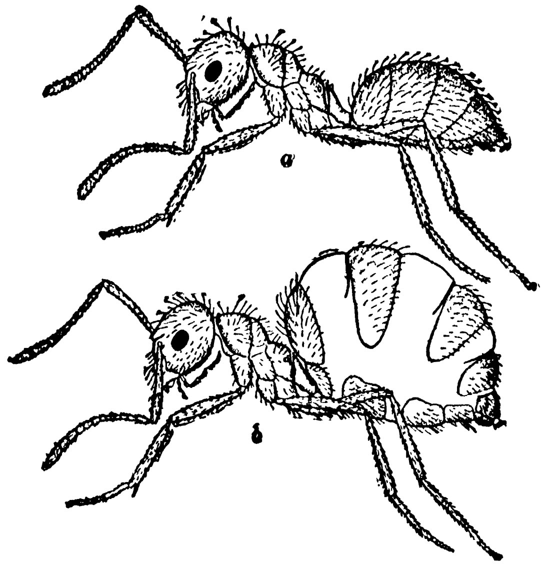


FIG. 562.—*PRENOLEPIS IMPARIS.*

a, worker in ordinary condition; *b*, replete. *After* Wheeler, "Ants."

In the sub-families Formicinæ and Dolichoderinæ the habit of collecting nectar and honey-dew has become highly developed. The workers of these insects have a pliable integument, which often allows of great distension when their crops are gorged with food. In many cases, the gorging may take place to such an extent that the inflated crop may cause the sclerites of the gaster to be so far forced apart that they appear as islands upon the tense intersegmental membranes: individuals which exhibit this habit are known as *repletes* (Fig. 562), and the species possessing this physiological caste are termed honey ants. In *Prenolepis* all the workers are thus able to distend themselves, and regurgitate the sweet substance which they collect to their larvæ or their sister ants. The true or perfect repletes are developed only in the nest, where they remain and store the sweets brought to them by the foragers, thus functioning as living casks or bottles. The contents of the latter are regurgitated when required for feeding the community. Repletes occur among the ants of N. America, S. Africa, and Australia but the caste is wanting in the British species.

The relations of ants to aphides and Lycænid larvæ represent only one of the many phases of symbiosis. There remain to be mentioned the many other phases which, unlike those already referred to, obtain *within* the nest. These are extremely diversified and the ants are, as a rule, passive or indifferent, and the other insects associated with them are mostly of the nature of inquilines. When the latter regularly inhabit the ants' nests, either throughout life, or during some stage in their development, they are known as myrmecophiles or ant-guests. Our knowledge of these organisms is due to the efforts of many workers, notably Wasmann, Escherich, Janet, Silvestri and others. Wasmann, in 1894, enumerated 1,246 species of myrmecophilous Arthropoda, the greater number being insects, and more especially Coleoptera. Since that time many more species have been brought to light, and we are now acquainted with probably over 2,000 species, including at least 1,200 different Coleoptera. In Britain there are about 300 species, upwards of 70 being Coleoptera. The relations of these myrmecophiles to the ants are extremely diversified, and the following classes are recognized by Wheeler. 1. The *synechthrans*, which live in the nests as scavengers or predators and are treated with marked hostility. They have to elude the ants in order to obtain their food, which usually consists of dead or diseased ants, the brood, or refuse of various kinds. They constitute rather a small group, comprising a number of agile carnivorous Staphylinidæ belonging to the genera *Mymedonia*, *Quedius*, *Xantholinus*, *Myrmœcia*, *Lamprinus*, etc. The first-mentioned genus is represented by numerous species on all the continents. 2. The *synœketes*, or indifferently tolerated guests, live in the nests without attracting the notice of the ants, or without arousing any obvious animosity. They are either too small, or too slow of movement, to attract attention, or have no specific odour which differentiates them. Among this large and heterogeneous assembly the most regular synœketes are the curiously flattened larvæ of the Syrphid genus *Microdon*. Verhœff has observed the fly ovipositing in the nest and it was repeatedly driven away by the ants (*Formica sanguinea*), but kept returning until the eggs were finally laid. In addition to *Microdon*, synœketes of British ants include Collembola of the genus *Cyphoderus*, larvæ of the Chrysomelid beetle *Clythra*, species of *Dinarda*, various Phoridæ, etc. A very large number of these guests are associated with the Doryline ants, accompanying the latter from place to place on their wanderings, and some of the Staphylinids, for example, exhibit an extraordinarily close mimetic resemblance to their hosts. The curious Lepismid *Atelura* is common in the nests of various European ants and, according to Janet, its members obtain most of their food by running up and imbibing some of the liquid while it is being regurgitated by one ant to another. The remarkable wingless crickets of the genus *Mymecophila*, and the diminutive cockroaches of the genus *Attaphila*, lick the ants in order to imbibe the cutaneous secretions of the latter, and often mount the bodies of their hosts in the process. 3. The *symphiles*, or true guests, are species which are amicably treated, licked, fed, and even reared by the ants. They are much less numerous than the synœketes, and consist largely of Coleoptera. Although they belong to many different families of the latter order, they exhibit marked adaptive convergence which is shown in the similarity of coloration, antennal characters, mouth-parts, and gland structure. These features are developed in order to solicit food from the ants, and to ingratiate themselves by means of special exudations. These true guests are assiduously licked by the ants, and it has long been known that they usually bear tufts of reddish or golden yellow hairs. The latter are regarded by Wasmann as being the most characteristic organs of the symphiles, and he has shown that they are situated on various regions of the integument, where numerous glands open, and that they have the function of diffusing some aromatic secretion. It is thus evident that the symphiles repay their hosts for their hospitality by secreting a substance which is highly attractive to them. Some of the most remarkable among the ant guests are the members of the *Lomechusa* group of the Staphylinidæ. These insects are tended with the greatest fidelity by the ants, who also rear the *Lomechusa* larvæ like their own brood notwithstanding the fact that the guest larvæ devour large numbers of both the eggs and young of their hosts. The Paussidæ and Clavigeridæ, which are remarkable for the bizarre forms assumed by their antennæ, also include among their ranks various symphiles. 4. The remaining groups of myrmecophilous insects are *parasites.* The latter include various larval Chalcids such as *Orasema* and other Eucharine genera, the Phorid *Metopina* and the Gamascid mite *Antennophorus.* The endoparasites include members of all the great groups of parasitic Hymenoptera, the Stylopid *Myrmecolax,* several Phoridæ and Conopidæ, and the Nematode *Mermis.*

So far reference has only been made to the relations of ants to other organisms. There are, however, many instances of social symbiosis between different species of ants. Thus two species of ants belonging to different genera may occupy a compound nest and live amicably together though keeping their broods separate. Other cases have been brought to light by Forel in which small ants nest in close proximity to larger species, and either feed upon the refuse food of the latter, or waylay its workers and compel them to deliver up their booty. True inquiline species are also known which can only live in association with a host of another species and share its nest. Social symbiosis leads us to the condition termed temporary social parasitism. In the latter type of existence the queen seeks adoption in the colony of another species and trusts to the alien workers to rear her first brood of young. The full benefits of this form of parasitism can only be secured by elimination of the queen of the host species. The workers of the latter gradually die out and the nest is ultimately entirely peopled by the parasitic ants. Parasite and host are always members of the same or closely allied genera.

From temporary social parasitism the next step is exhibited by dulosis or slavery. Slave-making ants are confined to the northern hemisphere and are members of four genera only. One of the best known species is the blood-red robber ant (*Formica sanguinea*) of Europe and N. America, which utilizes as its slaves certain other species of its genus, viz. *F. fusca* and its allies. An army of *sanguinea* workers start out and, having found a suitable nest, they do not kill the workers of the slave species unless they should offer resistance, their main object being to capture the pupæ and bring the latter back to their nest. It appears probable that a number of the captured pupæ are eaten since the number of slaves in a *sanguinea* nest is smaller than the number of cocoons captured. The survivors from the latter emerge and become slaves in the colony of the captors. Wasmann regards this species as a facultative slave-maker, since independent slaveless nests do occur, and there is nothing to show that the slaves are anything more than auxiliary rather than essential workers, in the colony which has adopted them. Obligatory slave-makers or "amazons" are members of the genus *Polyergus.* The European *P. rufescens* is one of the best known, and its normal slaves belong to the same species as those selected by *sanguinea.* The *Polyergus* never excavates its nest, or cares for its young, and is entirely dependent on the slaves hatched from the worker cocoons pillaged from the alien colonies. The European ant *Anergates atratulus* is a highly specialized social parasite, it possesses no workers, and selects as its host *Tetramorium cæspitum.* The *Anergates* queen enters the nest of the latter, and the eggs which she lays gives rise to a progeny which is tended and fed by the host workers. Ants which exhibit this parasitic habit are known to eliminate the queens of their host species which accept the alien substitutes. This mode of life is associated with degeneration ; the males of *Anergates*, for example, are sluggish, wingless ergatoid individuals, and more or less pupa-like ; the females are also modified and have rather poorly developed eyes.

Ants are frequently a great nuisance to man but are rarely actually destructive to any of his operations. One of the best known of the noxious species is the Argentine ant (*Iridomyrmex humilis*) which has overrun the warmer parts of the United States and become a serious household pest.

The literature on ants is voluminous but much of what is known concerning these insects will be found in the works of Wheeler (1910, 1922, 1923) which are accompanied by very full bibliographies. The two masters of European myrmecology are Forel and Emery, a mere list of whose writings would occupy several pages. Almost equally numerous are the various papers of Wasmann, particularly with reference to myrmecophilous insects. British ants number 34 species and these are admirably dealt with by Donisthorpe (1927), who has also described their myrmecophiles.

Superfamily **Vespoidea**

PRONOTUM EXTENDING BACK TO THE TEGULÆ. TROCHANTERS ALMOST ALWAYS ONE-JOINTED. PETIOLE OF ABDOMEN SIMPLE WITHOUT A SCALE OR NODE. APTEROUS FORMS FREQUENT : WORKERS WHEN PRESENT ALWAYS WINGED.

Included in this superfamily are the Diploptera, which comprise the true social and solitary wasps, and a number of families of solitary species which, together with the Sphecoidea, are often known as the Fossores. The habits of the members of this superfamily are extremely diversified : some are true endoparasites, others are ectoparasites, a few are inquilines, while the true wasps are essentially predaceous and insectivorous. The Masarinæ are the only group which includes species whose larvæ are regularly nourished upon a non-carnivorous diet, and are not inquilines in the nests of other species. The series of papers by Ashmead (1900, 1902, 1903) deal with the system of classification which has been partly followed in the present work.

Table of families :

1 (2).—Trochanters 2-jointed. TRIGONALIDÆ (p. 597)
2 (1).—Trochanters 1-jointed.
3 (4).—Wings almost always longitudinally folded in repose : pronotum with postero-lateral lobes angulated and extending above tegulæ. VESPIDÆ (p. 598)
4 (3).—Wings not folded longitudinally in repose : lobes of pronotum extending in front of or below tegulæ.
5 (14).—First abdominal sternum not separated from the second by a deep constriction or transverse furrow.
6 (7).—Legs fossorial : posterior pair long, femora usually reaching to or beyond apex of abdomen. POMPILIDÆ (p. 601)
7 (6).—Legs generally non-fossorial : posterior pair short, femora rarely reaching to or beyond apex of abdomen.
8 (9).—Abdomen with only three to five visible terga, the terminal segments tubular and retractile. CHRYSIDIDÆ (p. 598)
9 (8).—**Abdomen with at least six visible terga, the terminal segments not tubular and retractile.**

10 (11).—Hind-wings with distinct venation and without anal lobe: females never apterous. SAPYGIDÆ (p. 597)
11 (10).—Hind-wings without distinct venation and with an anal lobe: females often apterous.
12 (13).—Head not transverse: tarsi normal: antennæ 12–13-jointed. BETHYLIDÆ (p. 597)
13 (12).—Head transverse: fore tarsi in female almost always chelate: antennæ 10-jointed. DRYINIDÆ (p. 597)
14 (5).—First abdominal sternum separated from the second by a deep constriction or transverse furrow.
15 (16).—Middle coxæ usually widely separated. SCOLIIDÆ (p. 596)
16 (15).—Middle coxæ contiguous or nearly so.
17 (18).—Female winged; ocelli present. Abdomen with a long petiole. RHOPALOSOMIDÆ (p. 596)
18 (17).—Female apterous; ocelli often absent. Abdomen without a long petiole.
19 (20).—Middle coxæ usually slightly separated by a triangular or bilobed projection of the mesosternum: females with the thorax divided into three parts. THYNNIDÆ (p. 596)
20 (19).—Middle coxæ contiguous.
21 (22).—Hind-wings with an anal lobe: hypopygium of male with an aculeus: thorax of female divided into two parts. MYRMOSIDÆ (p. 596)
22 (21).—Hind-wings with no anal lobe: hypopygium of male unarmed, genital plate with two spines; thorax of female undivided. MUTILLIDÆ (p. 596)

FAM. MUTILLIDÆ.—The members of this family are characterized by a velvety body-pubescence and are black, brightly marked, or ringed, with yellow, orange, or red. The family is almost world-wide but apparently most abundant in S. America and the genus *Mutilla* ranges into both hemispheres (vide Mickel, 1928). All are parasites and have been reared from the cocoons of solitary bees and wasps as well as from the puparia of *Glossina*. The females are always apterous and are more commonly met with than the males: they are agile runners and can inflict painful stings. In a few species the males have the wings reduced to small pads or entirely wanting. Accurate field observations are necessary before it is possible to correctly associate the two sexes of most of the described species, as they are very different in form and coloration. Two species of *Mutilla* occur in Britain, one of which, *M. europæa*, is found in nests of *Bombus*.

FAM. MYRMOSIDÆ.—This small family is closely allied to the Mutillidæ and is regarded by André and other authorities as a sub-family of the former. The only British species is *Myrmosa melanocephala* F. which chiefly occurs in sandy localities in the south of England and is stated to be a parasite of *Oxybelus*: the male is entirely black and the female red with a black head and a yellow-banded abdomen.

FAM. THYNNIDÆ.—These insects are also closely allied to the Mutillidæ and exhibit even greater divergence of structure in the two sexes. The single British species, *Methoca ichneumonoides* Latr., occurs in the south of England but is rare and its female is liable to be mistaken for an ant. The genus is widely distributed and its prey consists of *Cicindela* larvæ which are partially or completely paralysed by stinging (vide H. G. and R. J. Champion, *Ent. Month. Mag.*, 50, 1914: Williams, 1919). The extensive genus *Thynnus* is chiefly Australian.

FAM. RHOPALOSOMIDÆ.—The remarkable Ichneumon-like insect *Rhopalosoma poeyi* Cress. (N. America and W. Indies) is the chief representative of this family, and according to Hood its larva is an ectoparasite of the tree-cricket *Orocharis*. Its systematic position has given rise to much difference of opinion and the insect has been variously placed in the Parasitica, the Spheciidæ and the Vespidæ. For a discussion of its affinities vide Ashmead (*Proc. Ent. Soc. Washington*, 1893).

FAM. SCOLIIDÆ (Fig. 563).—This extensive family includes the largest members of the Vespoidea. They are hairy insects whose prevailing colour is black marked with spots or bands of yellow or red, and the wings are often fuscous with a green or purple iridescence. They are mainly inhabitants of warm countries, and are ectoparasites of larval Scarabæidæ and probably of other of the larger coleopterous larvæ. Ashmead divides the group into four distinct families—the Cosilidæ, Tiphiidæ, Scoliidæ and Myzinidæ, but, for purposes of the general student, the older system of retaining these divisions as sub-families of the single family Scoliidæ is followed here. The only British genus is *Tiphia* of which the species *femorata* F. is recorded as a parasite of *Rhizotrogus*: several N. American members of the genus parasitize larvæ of *Lachnosterna*. The habits of certain species of *Scolia* have been observed by Fabre, and the females penetrate the ground in order to discover the Lamellicorn larvæ upon which they deposit their eggs. Thus *S. bifasciata* Ros. selects those of species of *Cetonia*, S. (*Elis*) *interrupta* F. chooses *Anoxia* and *S. flavifrons* F. is confined to *Oryctes* as its host. Fabre attaches great importance to the details of the stinging process and, in the case of *Cetonia*, the sting enters the latter in the mid-ventral line, at the junction of the pro- and mesothorax, in order to paralyse the motor centres of the body. There is, however, very little exact information with regard to the process of stinging.

FAM. SAPYGIDÆ.—The species of this family mostly frequent decaying wood and live in the nests of *Osmia*, *Sceliphron*, *Xylocopa*, etc. Although stated to be parasites some species at least are known to consume the food stored by their hosts rather than the progeny of the latter. Thus, according to Fabre, *Sapyga 5-punctata* is an inquiline which consumes the food which its host (*Osmia*) has laid in store. This species and *S. clavicornis* occur in Britain.

FAM. TRIGONALIDÆ.—A small family of very rare but widely distributed insects which are comprised in 17 genera and about 40 species. They are often included among the Parasitica on account of their multiarticulate antennæ and the 2-jointed trochanters. The ovipositor, though much reduced, issues from the apex of the abdomen and the venation is of the aculeate type. According to Clausen (*Proc. Ent. Soc. Washington*, 1931, p. 72), the eggs are laid on foliage and are swallowed by caterpillars of sawflies and Lepidoptera. They hatch into spinose larvæ and require as their true hosts larvæ of Ichneumon or Tachinid parasites. Those which occur in unparasitized caterpillars presumably perish. Trigonalids have also been bred from the cells of Vespoidea but the host-relationship is uncertain. The family has been monographed by Schultz (*Gen. Insectorum*, 61) and Bugnion (*Mitt. Schw. Ent. Ges.* 12) discusses certain anatomical features. Only a single species occurs in Britain.

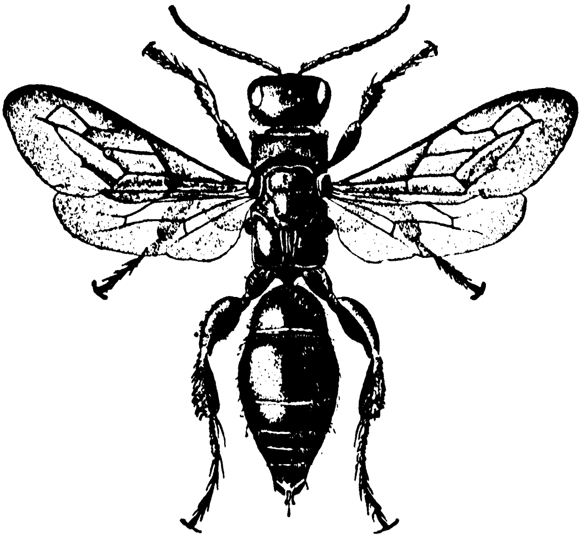


FIG. 563.—*Tiphia transversa*, Say. N. America. Female.

After Davis, *Bull. Illin. Nat. Hist. Survey* 13, Art. V. (reduced).

FAM. BETHYLIDÆ.—This family is sometimes united with the next to form the superfamily Bethyloidea. Both comprise very small insects linking the Vespoidea with the Proctotrypoidea. In the Bethylidæ the females are often apterous and very different from the males so that the sexes are not easily correlated: in *Sclerodermus* both sexes include winged and apterous individuals. So far as known the species of this family parasitize lepidopterous and coleopterous larvæ and their biology has been chiefly observed by Bridwell (*Proc. Hawaiian Ent. Soc.* 3, 4) and by Williams (*Ibid.* 4). *Epyris* stings Tenebrionid larvæ and lays a single egg on each: *Sclerodermus* utilizes various coleopterous larvæ distributing her eggs over the prey, while *Goniozus* and its allies attack concealed lepidopterous larvæ. Parthenogenesis has been recorded among these insects, the unfertilized eggs producing males.

FAM. DRYINIDÆ (Fig. 564).—The members of this family are easily recognized by the anterior tarsi in the female being chelate (except in *Aphelopus* and its allies): as in the preceding sub-family, the females are frequently apterous. All are parasitic upon the nymphs of Homoptera and more especially those pertaining to the families Fulgoridæ, Cercopidæ, Membracidæ, and Jassidæ. Their biology is of exceptional interest and most of what is known thereon will be found in writings of Perkins (*Hawaiian Sugar Pl. Ass.*, Bulls. 1, 4, 11), Fenton (*Ohio Journ. Sci.* 28, no. 6, 1918), Kornhauser (*Journ. Morph.* 1919) and Keilin and Thompson (*C.R. Soc. Biol. Paris*, 1915). During the larval stages they are endoparasites in the abdomen of the host and, sooner or later, an external gall-like cyst or thylacium containing the parasite is developed as a proliferation of the integument of the attacked insect. This cyst protrudes after the manner of a hernia, its position on the host is variable, and one or several may be present on a single individual. In many cases the cyst may be as large as the abdomen of the host, and is usually black or yellow in colour. Pupation takes place either on the food-plant of the Homopteron or in the soil. The effect of the parasitism is often very marked and the changes induced are regarded by Giard as an instance of "castration parasitaire." They vary according to the species of insect attacked and, in some cases, they are evident externally owing to the imperfect development of the genitalia of the host. Over 300 species of Dryinidæ are known and the greatest number have been described from Europe: in Britain *Aphelopus* frequently parasitizes species of *Typhlocyba* and *Chlorita*.

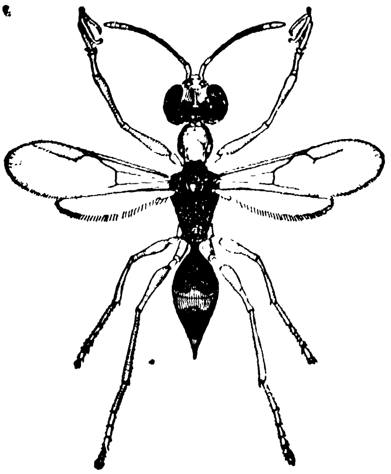


FIG. 564.—*ECHTHRODELPHAX FAIRCHILDI*, FEMALE.

After Perkins, *Ent. Bull.* 11. *Hawaiian Sugar Pl. Assn.*

FAM. CHRYSIDIDÆ.—(Cuckoo wasps or ruby-tailed wasps.) These insects are of a brilliant metallic coloration, generally green, green and ruby, or blue, with a very hard coarsely-sculptured integument. They are easily recognizable by the structure of the abdomen, which is peculiar in several ways, and very little longer than the head and thorax. It is convex above, and flat or concave beneath, so that it is capable of being readily turned under the thorax and closely applied to the latter. In this manner the insect rolls itself into a ball when attacked, leaving only the wings projecting. There are, with few exceptions, only three or four segments visible dorsally. The terminal segments in the female are modified to form a retractile tube within which the ovipositor is concealed (Fig. 565). The imagines only fly during hot sunshine, and are usually seen in the neighbourhood of the nests of various solitary bees and wasps within which their transformations take place. The family is very widely distributed and the genus *Chrysis* includes over 1,000 species. About 24 species of Chrysididæ are British, one of the commonest being *Chrysis ignita* (vide Morice, *Ent. Month. Mag.* 36). So far as known all the species are parasites, or less frequently inquilines, and the Eumenidæ and Megachilidæ are especially subject to their attacks: *Cleptes*, however, is exceptional in that it parasitizes Tenthredinidæ. As a rule their larvæ prey on those of the host but Chapman (*Ent. Month. Mag.* 6) has observed the larva of *Chrysis ignita* feeding upon a caterpillar stored by its host (*Odynerus*). The genus *Cleptes* is also, in other ways, anomalous: the male has five visible abdominal segments and the female, unlike other members of the family, is provided with poison glands and is capable of stinging. For further information on the Chrysididæ reference should be made to the contribution of du Buysson in the work of André (1879).

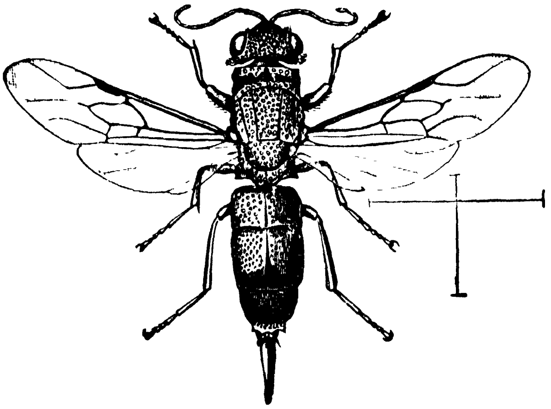


FIG. 565.—*CHRYSIS IGNITA*, FEMALE. BRITAIN.

After Sharp, *Camb. Nat. Hist.*

FAM. VESPIDÆ.—The largest and most important family of the Vespoidea, comprising the social and solitary true wasps. It is divided into nine sub-families of which the Vespinæ are the only social wasps found in Europe. Of the solitary families, the *Masarinæ* have the antennæ apically thickened or clubbed and the wings are never longitudinally plicate, or imperfectly so. They construct nests in the form of tubular cells disposed side by side in the earth or in dry stems. Their arvæ are fed with a paste of pollen and honey, except in *Pseudomasaris* which stores ts cells with caterpillars. Although widely distributed the sub-family does not occur in Europe.

The *Eumeninæ* comprise most of the solitary wasps of temperate regions. They exhibit many variations in nest-building habits: certain species dig tunnels in the ground, and others construct tubular nests in wood or stems, partitioning the tunnels nto cells divided by mud walls. There are, furthermore, a number of species which are mason or potter wasps, constructing oval or globular vase-like nests of mud or clay fastened to twigs and other subjects. The latter types are often of the daintiest description and are said to have served as models for early Indian pottery. The species of *Odynerus* construct varied kinds of nests, while some regularly take advantage of a deserted nest of another wasp, or of a nail-hole or key-hole, rather than build cells of their own. All the species of the family are predaceous upon small epidopterous larvæ, or more rarely, upon those of the Tenthredinidæ and Chrysomeidæ, and are of economic importance. The prey when captured is stated by Fabre to be stung into insensibility and a dozen or more larvæ may be stored in a single cell. The wasp deposits each egg by means of a suspensory filament from the roof of the cell where it hangs in close proximity to the food thus collected and, after the chamber is sealed, the parent betrays no further care for its offspring. The family s a large one well represented in most regions of the globe and its habits are discussed by Roubaud (1916), Williams (1919) and others. Two genera occur in Britain, viz. *Eumenes* and *Odynerus*. In the former the first abdominal segment is very long, and narrowed nto a petiole (Fig. 566) while in *Odynerus* the petiole is scarcely evident.

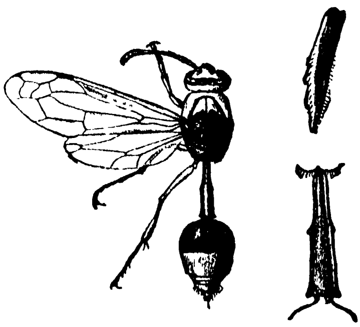


FIG. 566.—*EUMENES PETIOLATA.* FEMALE × 5/6. INDIA.
After Bingham (F.B.I.).

The *Vespinæ* occur in all continents excepting S. America and a large part of Africa. This subfamily, in temperate regions, includes the papermaking wasps which are social in habit, and live n large communities each composed of a fertilized female or "queen," workers, and males. The colonies exist for a single season only, the males and workers perishing during autumn, while the mpregnated females hibernate and each founds a new colony the next spring. The three forms of individuals are very alike in coloration, but the queens are considerably larger than the workers and males: the males may be readily distinguished by having seven evident abdominal segments and thirteen joints to the antennæ, whereas only six abdominal segments and twelve antennal joints are found in the queens and workers. Vespidæ are argely predaceous in habit and feed their larvæ upon other insects, portions of which they previously masticate: both fresh and decaying meat and fish are also utilized. The adult wasps are very partial to nectar, ripe fruits and honey-dew and this same diet is given to the very young larvæ for a short period. Their mouthparts have not attained the length and perfection found among bees, and hence wasps are unable to obtain the secretions of deeply seated nectaries. Although, at times, they cause injury to fruit they render service as scavengers and in reducing the numbers of other insects, more especially Diptera and lepidopterous larvæ. All the British species of the family belong to the genus *Vespa* and our knowledge of these insects has been greatly extended by the researches of Janet (1893, etc.) and Marchal (1896). Great variety of nest construction is found in this genus and the British forms exhibit three distinct types of nidification. Thus *Vespa vulgaris, germanica,* and *rufa* make underground nests; *V. sylvestris* and *norvegica* suspend their nests from bushes, trees, etc., while *V. crabro* (the hornet) nests in hollow trees or more rarely in banks. *V. austriaca* (*arborea*) is a race of *V. rufa* in whose nests it is occasionally present as an inquiline. The stings of these insects are always painful and many of the tropical species are very fierce and easily roused, their stings sometimes involving dangerous consequences to animals and human beings. One of the largest species of the genus s the Himalayan *V. ducalis* Sm. whose queens attain a length of 40 mm. with a wing-expanse of over 80 mm.

After hibernation the female wasps are roused into activity by the warmth of early spring, and commence to seek out likely situations for their nests. Having discovered suitable places they proceed to gather the material for nest construction. This consists of weather-worn but sound wood, particles of which are rasped off by means of the mandibles, and worked up with the aid of saliva to form a substance known as "wasp-paper." In the case of *V. germanica* and *vulgaris*, layers of the substance are applied to the roof of the cavity in the ground destined to hold the nest. From the centre of the disc thus formed, a pedicel is hung with its lower end widened out. Upon the latter the first cells, up to about thirty in number, are constructed: they are hexagonal in form, open below and closed above. An umbrella-like covering is suspended from the roof of the cavity to protect the comb and, in the angle of each cell nearest the centre of the comb, an egg is deposited, being fixed by means of a cement-like substance. In a few days, according to temperature, the larvæ hatch and are fed by the parent until ready to pupate. Prior to transforming the larva spins a cocoon within the cell and closes the mouth of the latter with a tough floor of silk. The contents of the gut are now evacuated for the first time, and transformation into the pupa takes place. After a period of four to six weeks from the time of egg-laying, the adult wasps bite their way through the floors of their cells and emerge. These individuals are always workers, and very soon the entire care of the young and the nest-building is taken over by them, the parent female devoting herself solely to egg-laying. When the nest is fully formed (Fig. 567) it is more or less spherical in form externally, and is invested by several layers of coverings which protect it from rain and also serve to prevent loss of heat from within. New cells are added at the periphery of those already formed and, when one layer of comb has attained a suitable size, new tiers or layers are built below and interconnected with vertical pillars. This goes on until about seven or more combs are constructed and the spaces between the several combs, and between these and the innermost covering of the nest, are just sufficient to allow of the free movement of the occupants of the nest. Each cell of the comb is used for rearing the brood twice or perhaps three times, and it will therefore be seen that the number of cells does not accurately represent the total population of a colony. Janet found in a nest containing seven combs 11,500 cells of which 11,000 had been used twice and the remainder thrice. An average sized nest probably has a population of about 5,000 individuals towards the end of the season. Near the end of summer larger cells are constructed and these "royal" cells are destined for the females or "queens" of the next generation. The fertilized eggs produce either females or workers, depending upon the amount of food supplied to the larvæ. When food is particularly abundant, or in nests which require re-queening, the workers undergo increased development and become fertile but are structurally incapable of impregnation. Males are always produced from unfertilized eggs whether the latter be laid by the female or workers.

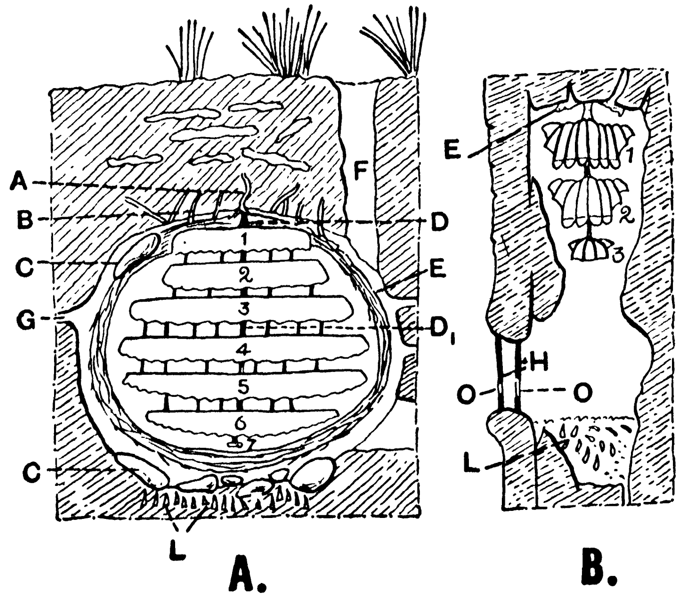


FIG. 567.—A, SECTION OF SUBTERRANEAN NEST OF *VESPA GERMANICA*; B, SECTION OF NEST OF *V. CRABRO* IN A TREE-HOLLOW.

A, root to which first attachment *D* was made; *B*, secondary attachment; *C*, pieces of flint; D_1, suspensory pillar; *E*, envelope, in **B** its vestiges; *F*, entrance; *G*, side gallery; *H*, lamellæ closing opening to tree hollow; *O*, entrance orifices in lamellæ; *L*, saprophagous dipterous larvæ. The numerals refer to layers of comb in order of construction. Adapted from Janet.

In addition to their normal occupants a large number of other insects have been observed in wasps' nests, either as parasites or inquilines. In the soil beneath the nest, which contains excreta and other organic matter, larvæ of *Pegomyia* (*Acan-*

thiptera) *inanis* are often abundant. Larvæ of *Volucella inanis*, *zonaria* and *pellucens* appear to act as scavengers devouring excreta, etc., and doing no harm to the occupants of the cells : among true parasites the most important is *Metœcus paradoxus* which destroys the larvæ. Newstead (*Ent. Month. Mag.* 1891) has recorded a number of other insects and several species of Acari from nests of *V. germanica* and *V. vulgaris*.

Polistes is the only other European genus : its colonies are much smaller than those of *Vespa*, and each nest is composed of a single tier of cells suspended by means of a central pedicel, without any external envelope.

Of the extra-European sub-families of solitary species little is known about the *Euparaginæ*. The *Zethinæ* show an advance on the Eumeninæ in that they incorporate wood or other plant material in forming their cells and some species practise progressive provisioning. Of the extra-European social groups the *Stenogastrinæ*, of the Orient and Australia, are the most primitive. Some species are solitary and others social : the latter make fragile naked combs, the colony comprises but few individuals, and the larvæ are fed by progressive provisioning. The *Polybiinæ* are the largest social group : they are tropical and largely S. American. In species of *Belonogaster* in Africa the colonies are small and there is a rude division of labour, the older females being the egg-layers and the younger individuals are foragers : new colonies are provided for by rudimentary swarming. In the higher genera true queens and workers prevail : the colonies are immensely populous and polygynous, while swarming is a regular phase in their life. In *Nectarina* honey forms part of the nest provisions. The *Ropalidiinæ* are a small group found in the tropics of the old world : they are primitive forms constructing naked combs and there is little or no distinction into queens and workers.

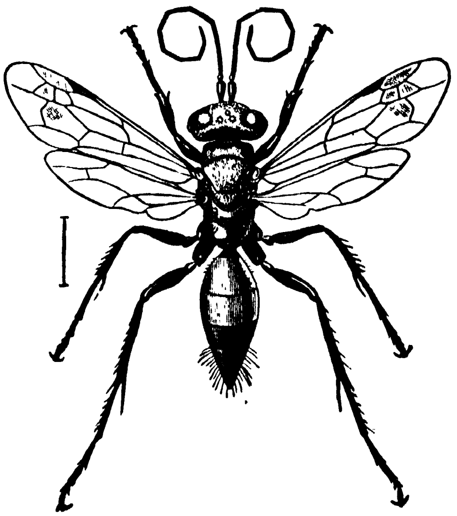


FIG. 568.—*CALICURGUS HYALINATUS*, FEMALE. BRITAIN.

After Sharp, *Camb. Nat. Hist.*

Among the principal works on the family is De Saussure's monograph (1853–58) and the writings of Janet, Marchal, Roubaud (1916), Bequaert (1918) and Dalla Torre (*Gen. Insectorum* 19) : for a useful account of the biology of the British Vespidæ vide Latter (1904). Their evolution and economy are fully discussed by Wheeler (1928).

FAM. POMPILIDÆ (Psammocharidæ).—The Pompilidæ are the most extensive group of the Vespoidea and are distributed over almost the whole world ; six genera, including about 30 species, are found in the British Isles (vide Perkins, *Ent. Month. Mag.* 1920). In these insects the abdomen is devoid of a definite pedicel, the hind pair of legs is very long and the males are more slenderly built and usually smaller than the females (Fig. 568). All are fossorial and predatory wasps, their size is very variable and certain species may attain a length of three inches. Included in the genus *Salius* are some of the largest of all Hymenoptera. They are remarkable for their extreme activity and possess great powers of running. The nests of these insects are usually burrows in the ground, but *Agenia* constructs earthen vase-like receptacles which are attached to walls or stones. Their prey consists almost exclusively of spiders and some of them, by means of their highly developed stinging powers, are able to overcome even the largest of these Arachnids. One of the giants of the family is *Pepsis femoratus* which stores its burrows with the great Tarantula spiders. The habits of the Pompilidæ have been observed by Fabre (*Souv. Ent.* 4th ser.), the Peckhams (1898), Ferton (1901–21), Williams (1919) and others. There appears to be a good deal of variation in the degree of perfection in the art of stinging among different species. Fabre states that *Calicurgus* first stings its prey between the poison fangs of the latter, and subsequently near the junction of the cephalothorax and abdomen, thereby producing complete immobility. The observations of the Peckhams on species of *Pompilus* indicate that in this genus stinging is a much less refined process : in some cases the spider is stung in such a way that it is killed outright, while in others it may live for 40 or more days, but in all cases it is reduced to a sufficiently helpless condition to afford a safe repository for the egg of the wasp.

Superfamily **Sphecoidea**

PRONOTUM NOT EXTENDING BACK TO THE TEGULÆ. TROCHANTERS ONE-JOINTED, HIND TARSI SLENDER, NOT DILATED. PUBESCENCE OF HEAD AND THORAX SIMPLE NOT PLUMOSE. WORKERS AND APTEROUS FORMS ABSENT.

This superfamily is composed of fossorial wasps and none exhibit any true social life. For the most part they may be regarded as beneficial insects from the fact that they are predaceous and store their nests with lepidopterous larvæ, Hemiptera-Homoptera, Orthoptera, Araneida, etc. Parental care for their larvæ occurs in species of *Bembex* and *Philanthus* but, for the remainder, once the cells have been provisioned, and an egg deposited in each, they are sealed down and the parent exhibits no further concern for her offspring. As a general rule they sting their prey before storing the latter in the larval cells, and the result of the stinging in most cases is to induce rapid paralysis of the motor centres, thereby eliminating all or almost all power of movement. The often repeated assertion that the prey is stung in the ganglionic nerve centres is not an ascertained fact, but an inference drawn from the effects of stinging, and the positions in which the sting is inserted into the bodies of the victims. In a number of cases the prey is stated to be killed outright, but it retains its fresh condition for a variable period up to several weeks, a fact which suggests the possibility that the injected venom exercises an antiseptic influence. Many interesting and original observations on the habits and instincts of the European species of the group are detailed in the writings of Fabre and of Ferton; a number of the American species have been studied by G. W. and E. G. Peckham and certain of the African forms by Roubaud (1916). Kohl (1896), who is the European authority on the classification of these wasps, regards them as forming a single family, but the work of Ashmead and others has shown that the Sphecoidea are a complex group divisible into a number of families which exhibit different structure and habits.

Key to the families:

1 (14).—Middle tibiæ with one apical spur, rarely with none.
2 (5).—Fore-wing with one cubital cell: median cell in hind-wing twice as long as sub-median.
3 (4).—Head transverse; postscutellum with a spine or forked process and with squamæ. OXBELIDÆ (p. 605)
4 (3).—Head quadrate: postscutellum unarmed and without squamæ. CRABRONIDÆ (p. 605)
5 (2).—Fore-wing usually with two or three cubital cells: median cell in hind-wing not twice as long as sub-median.
6 (11).—Abdomen with no marked constriction between segments 1 and 2.
7 (8).—Abdomen petiolate or subpetiolate. PEMPHREDONIDÆ (p. 605)
8 (7).—Abdomen sessile.
9 (10).—Labrum large and well developed, ocelli aborted and represented by scars. BEMBECIDÆ (p. 605)
10 (9).—Labrum small, concealed, ocelli distinct or never all aborted. LARRIDÆ (p. 605)
11 (6).—Abdomen with a strong constriction between segments 1 and 2.
12 (13).—Head wider than the thorax: fore-wing with 3 cubital cells: abdomen rarely petiolate. PHILANTHIDÆ (p. 604)
13 (12).—Head not wider than the thorax: fore-wing with 1 or 2 cubital cells: abdomen petiolate. TRYPOXYLONIDÆ (p. 604)
14 (1).—Middle tibiæ with two apical spurs.

15 (16).—Abdomen with a constriction between segments 1 and 2: middle coxæ contiguous. MELLINIDÆ (p. 604)

16 (15).—Abdomen with no constriction between segments 1 and 2: middle coxæ not contiguous.

17 (22).—Mesosternum normal; mesonotum without parapsidal furrows.

18 (21).—Abdomen sessile or subsessile.

19 (20).—Labrum not free, covered by the clypeus: transverse median vein usually straight. NYSSONIDÆ (p. 604)

20 (19).—Labrum free, well developed: transverse median vein usually sinuate. STIZIDÆ (p. 604)

21 (18).—Abdomen petiolate. SPHECIDÆ (p. 603)

22 (17).—Mesosternum produced into a forked process posteriorly: mesonotum with parapsidal furrows. AMPULICIDÆ (p. 603)

FAM. AMPULICIDÆ.—The members of this family are rare in individuals and few in species. The prothorax is narrow and elongate and the base of the abdomen is constricted to form a short pseudo-petiole. So far as known they are predaceous upon Blattidæ and Bingham mentions that in Burma they enter houses and search for their prey in likely situations. They do not form definite nests and, after having stung their prey into submission, the latter are dragged away and stored in any suitable hole or crevice (vide Williams, 1919). The family ranges into both hemispheres but is unrepresented in Britain. *Dolichurus* and *Ampulex* occur in France.

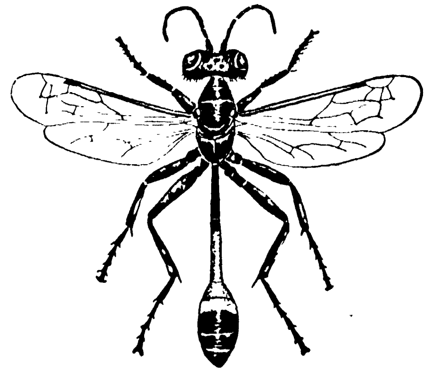


FIG. 569.—*Ammophila sabulosa*, Female. Britain, × 2.

FAM. SPHECIDÆ (*Sphegidæ*).—The members of this extensive family are slender wasps, with the propodeum elongate, and the petiole so much attenuated that it is often little stouter than a fine bristle, and it may exceed in length the remainder of the abdomen (Fig. 569). They are usually black insects with yellow or reddish markings, the legs are adapted for digging and running, and their methods of stinging are highly specialized. The best known genera are *Sphex* L. and *Ammophila* Kirby, which, as the Peckhams remark, include some of the most graceful and attractive of all wasps—not only on account of their form but also owing to their intelligence and individuality. The above-mentioned observers, and also Fabre, have studied their habits in detail and the records of their observations form some of the most remarkable chapters in insect biology. Stated very briefly, the prey consists either of lepidopterous larvæ or Orthoptera which are stored in a single cell situated at the termination of a vertical tunnel in the ground. The method adopted by these insects in stinging their prey is the most complex known and has been observed by Fabre in the case of *S. hirsutus* and by the Peckhams in *S. urnarius*. It is a multiple process but there is some variation with regard to the number of stings administered. In one instance Fabre mentions that stinging took place at twelve different points, beginning between the first and second segments and progressing backwards. In his second example, the third, second and first segments were stung in the order given and thereafter the remaining segments up to the ninth. In other cases he noted that usually all the segments were stung. After stinging had been accomplished the prey, in some instances, was subjected to a further process known as malaxation, which consists in repeatedly compressing the neck of the victim with the mandibles. The Peckhams' observations largely confirm those of Fabre with the exception that the middle segments of the prey, upon which the egg is deposited, were never touched, while in Fabre's observations they invariably were. They also noted that malaxation was most severe in the case of a caterpillar which was only stung once. It is evident from the various observations which have been recorded that the order in which the segments are stung, the number stung, and the subsequent malaxation which may occur are all somewhat inconstant. The poison introduced during stinging either paralyses or kills the prey and also acts as an antiseptic, keeping the tissues fresh for many weeks. As Wheeler observes, Fabre's and Bergson's contention that the insect is a clairvoyant surgeon, with an intuitive knowledge of the internal anatomy of its prey, may be dismissed as a myth. *Sceliphron* (*Pelopæus*) includes the " mud-daubers " whose nests are constructed of kneaded mud or clay and are composed of about 10 to 50 cells. These insects occur in most of the warmer regions of the globe and are very fond of building their nests in human habitations. Their prey consists of spiders and it appears to be a matter of indifference whether the latter be killed or only paralysed and either event may follow as the result of being stung. An examination made by the Peckhams of cells recently provisioned showed that while most of the spiders were dead, many clearly exhibited indications of being still alive. The latter died off from day to day and the dead Arachnids remained in good condition for a period of ten or twelve days.

FAM. STIZIDÆ.—These insects are often united with the Bembecidæ but may be distinguished from them by the presence of two apical spurs to the middle tibiæ and by the strongly defined constriction between the first and second abdominal segments. Comparatively little has been observed with regard to their habits beyond the fact that they are predaceous upon Orthoptera and Homoptera and construct burrows in the ground. In N. America *Sphecius speciosus* is a large and formidable insect preying upon cicadas ; its burrows extend for two feet or more in depth in sand, each is provisioned with a single cicada and pupation takes place in a silken cocoon with incorporated soil particles (vide Riley, *Ins. Life*, 4). Both *Sphecius* and *Stizus* are European but do not extend their range into Britain.

FAM. NYSSONIDÆ.—These wasps are medium-sized insects and some of them bear a remarkably close superficial resemblance to members of the Eumenidæ. Their prey consists of small Homoptera, particularly Cercopidæ. Both *Gorytes* and *Nysson* occur in Britain, and species of the former genus have been recorded as preying upon the nymphs of *Aphrophora spumaria.*

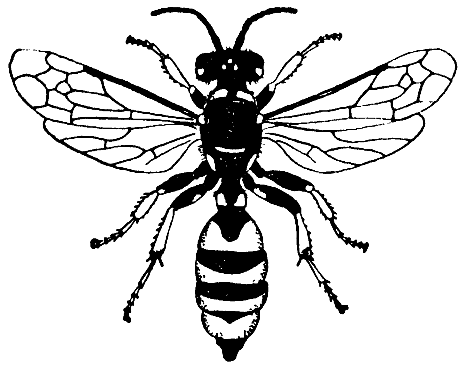


FIG. 570.—*CERCERIS ARENARIA*, FEMALE. BRITAIN, × 2·5.

FAM. MELLINIDÆ.—The few recorded observations on these insects indicate that they are predaceous upon Diptera. *Mellinus arvensis* is common in Britain and according to Smith it often resorts to patches of cow-dung in search of its prey. The species burrow in sand and their larvæ spin brown cocoons.

FAM. TRYPOXYLONIDÆ. — The best known genera in this family are *Pison* and *Trypoxylon,* the latter being represented in Britain by three species. Their nests are divided into cells separated by partitions, and they frequently utilize holes in posts, chinks in mortar and brickwork, decayed wood, plant stems, etc. Some species build clay or mud nests in or near houses, others utilize the abandoned nests of *Sceliphron,* or make burrows in the ground. For the most part they store their nests with spiders, but Ashmead records certain species as preying upon aphids. An account of the habits of *Trypoxylon albopilosum* and *T. rubrocinctum* is given by G. W. and E. G. Peckham (1898) and those of *T. politum* by P. and N. Rau (*Journ. Animal Behav.* 1916).

FAM. PHILANTHIDÆ.—These insects are burrowers in the earth and the species of *Philanthus* prey upon *Andrena, Halictus, Apis* and other Hymenoptera. The victim is stung on or near the under surface of the mentum and death rapidly supervenes. One of the best known species is *Philanthus triangulum* F. which commonly preys upon the hive bee. According to Fabre, after the bee has been stung it is subjected to vigorous malaxation for the purpose of forcing out the contained honey. The latter is imbibed by the captor and its extraction is stated to be necessary before the bee can be safely used as food by the larval *Philanthus.* Fabre states that the burrows of this species are about 3 feet deep and they terminate in the larval cells. The female bee supplies her brood with food from time to time and consequently tends her offspring after the manner of *Bembex.* The species of the extensive genus *Cerceris* (Fig. 570) make solitary nests in the ground and store them with adult Coleoptera or with bees of the genera *Halictus* and *Andrena.* According to Marchal *C. rybiensis* L. (*ornata* F.) preys upon *Halictus* and the latter is stung in very much the same manner as the prey of *Philanthus* and is afterwards subjected to malaxation. *C. bupresticida* Duf. confines itself to species of Buprestidæ while *C. Ferreri* Lind., *4-cincta* Vill., and *specularis* Costa prey upon Curculionidæ. According to Wheeler (*Journ. Animal Behav.*, 1913) *Aphilanthops frigidus* stores its nest with queen ants. The family is represented in Britain by *Philanthus triangulum* and six species of *Cerceris*.

FAM. LARRIDÆ.—The members of this family are burrowing wasps which inhabit sandy localities and provision their nests with Orthoptera and Hemiptera. The European species of *Tachytes* include among their prey *Mantis* and *Stenobothrus*; *Larra anathema* chooses *Gryllotalpa*, while *Tachysphex* stores its nests with *Gryllus* and various Acridiidæ. *Astata* and its allies are often regarded as a separate family; they mostly provision their nests with the nymphs of Pentatomidæ and other Hemiptera (Coreidæ and Lygæidæ) which they generally capture in the nymphal condition.

FAM. BEMBECIDÆ.—The Bembecidæ live in a semi-social manner, a number of individuals occupying a limited area of ground but each one has a separate nest. Thus Wesenberg (*Ent. Medd.*, 1891) states that fifty Bembecids will occupy an area about equal to that of an ordinary room. *Bembex* differs from almost all other solitary wasps in that the cells containing its larvæ are left unsealed and the latter are fed from day to day. The difference in maternal care entails very great industry on the part of the parent wasps and results in a much less numerous progeny. The prey consists of Diptera and among the genera recorded as serving this purpose are such relatively large forms as *Echinomyia*, *Eristalis* and *Tabanus*. In *Bembex rostrata* a single female supports five or six larvæ and each of the latter requires 50 to 80 flies during the fourteen or fifteen days spent in that stage. Parker (*Proc. U.S. Nat. Mus.* 52) discusses the biology of the family and believes that the parent wasps find their skilfully concealed burrows by olfactory sense. He mentions several instances in which the surface of the burrow was disturbed, and even water was poured over it, without causing the wasp to lose track of its nest. In addition to this work and that of Marchal the reader should also consult the writings of Fabre and G. W. and E. G. Peckham.

FAM. PEMPHREDONIDÆ.—Included in this family are a number of small black wasps of slender build which usually form irregular galleries in dry twigs or in the wood of posts and rails. Their chief prey consists of Aphididæ, but Psyllidæ and other small Hemiptera-Homoptera are also taken. *Pemphredon* consists of a number of very similar species of which five occur in Britain.

FAM. CRABRONIDÆ.—These insects form a large and important family of small species which exhibit extremely varied habits. The genus *Crabro* occurs over a large part of the world and constitutes the dominant group of fossorial Hymenoptera in Britain where it is represented by about 30 species. Their nests are constructed in stems of bramble, in palings and posts, in the ground and other situations. Diptera appear to form their chief prey but some species store their nests with lepidopterous larvæ or small Homoptera. There is a considerable amount of evidence indicating that different nesting habits and prey are directly associated with certain groups of species. The method of disabling the prey has been much discussed and stinging appears to be the usual process (vide Hamm and Richards, 1926).

FAM. OXYBELIDÆ.—This family includes certain small wasps which burrow in the ground in sandy places and provision their nests with Diptera and more especially with species of Anthomyidæ and Muscidæ. According to Verhoeff the prey is not stung but the thoracic nerve centres are crushed which results in paralysis. In the American species observed by the Peckhams the prey is stated to be intact, and more recent observers mention that stinging takes place. *Oxybelus* is represented in Britain by four species of which *O. uniglumis* L. is frequent and generally distributed.

Superfamily **Apoidea**

PRONOTUM NOT EXTENDING BACK TO TEGULÆ. TROCHANTERS ONE-JOINTED, HIND TARSI DILATED OR THICKENED. PUBESCENCE OF HEAD AND THORAX FEATHERY OR PLUMOSE. WORKERS SOMETIMES PRESENT; APTEROUS FORMS WANTING.

Included in this superfamily are the social and solitary bees. The truly social species, which have evolved a worker caste, are confined to the families Bombidæ and Apidæ, the great majority of forms being solitary. The adults are most important agents for pollinating flowers, the pollen adhering to the plumose body-hairs. The glossa is always well developed, generally pointed, and often exceedingly long. The food consists of nectar and pollen, the former supplying the carbohydrate ingredients and the latter the protein and hydrocarbons. The larvæ are fed upon a similar diet, except that the nectar is regurgitated as honey before being served to them. These substances are stored in the cells, and the latter are never provisioned with animal food. The females are provided with corbiculæ consisting of special pollen-collecting hairs which are situated either on the abdominal sterna, or on the posterior tibiæ and tarsi, or on the femora. Certain genera, however, notably *Nomada*, *Cœlioxys* and *Psithyrus*, are inquilines in the nests of other species, and corbiculæ are wanting in these instances. A useful account of the structure and biology of certain of the solitary bees is given by Semichon (1906). For the habits of these insects vide also Friese (1922–23), Ferton, Fabre and the literature quoted under the different families.

Key to the families:

1 (8).—Glossa flattened, usually shorter than mentum: basal joints of labial palpi cylindrical, not unlike succeeding joints.
2 (5).—Glossa short, broad, and obtuse or emarginate apically.
3 (4).—Small black bees with scanty pubescence: fore-wing with 2 cubital cells; hind femora in female without pollen brushes. PROSOPIDÆ (p. 607)
4 (3).—Moderate sized hairy bees: fore-wing with 3 cubital cells; hind femora in female with pollen brushes. COLLETIDÆ (p. 607)
5 (2).—Glossa long or short, apex acute: pollen brushes present.
6 (7).—Fore-wing with 2 cubital cells: glossa long, labrum large and not covered by clypeus. PANURGIDÆ (p. 607)
7 (6).—Fore-wing with 3 cubital cells: glossa shorter, labrum small and mostly concealed by clypeus. ANDRENIDÆ (p. 607)
8 (1).—Glossa very elongate, always longer than mentum: two basal joints of labial palpi elongate, compressed, and unlike succeeding joints.
9 (10).—Hind tibiæ without apical spurs. APIDÆ (p. 611)
10 (9).—Hind tibiæ with apical spurs.
11 (12).—Usually metallic bees, bare or nearly so: the glossa extending to or beyond middle of abdomen; maxillary palpi 1-jointed. EUGLOSSIDÆ (p. 609)
12 (11).—Not such bees.
13 (14).—Eyes well separated from bases of mandibles. BOMBIDÆ (p. 609)
14 (13).—Eyes reaching or almost reaching bases of mandibles.
15 (22).—Fore-wings with three cubital cells.
16 (19).—Radial cell neither markedly long nor narrow, rarely longer than first 2 cubital cells united.
17 (18).—Hairy pollen-collecting bees. ANTHOPHORIDÆ (part) (p. 609)
18 (17).—Sparsely hairy or bare parasitic bees, with no pollen-collecting apparatus. NOMADIDÆ (p. 609)
19 (16).—Radial cell long and narrow, as long as or longer than three cubital cells united.
20 (21).—Small bees, metallic or submetallic, nearly bare: hind tibia and tarsus of female without distinct scopa. CERATINIDÆ (p. 609)
21 (20).—Large bees with dense scopa: thorax thickly pubescent. XYLOCOPIDÆ (part) (p. 608)
22 (15).—Fore-wings with two cubital cells.
23 (26).—Labrum large and uncovered, hind-legs with a dense scopa.
24 (25).—Radial cell neither long nor narrow. ANTHOPHORIDÆ (part)

25 (24).—Radial cell very long and narrow. XYLOCOPIDÆ (part)

26 (23).—Labrum small and usually concealed by clypeus.

27 (28).—Abdomen in female with a ventral scopa: labrum entirely covered by clypeus. MEGACHILIDÆ (p. 608)

28 (27).—Abdomen in female without a ventral scopa: labrum not entirely covered by clypeus. STELIDIDÆ (p. 607)

FAM. PROSOPIDÆ.—A small family of bees whose principal genus is *Prosopis* F. (*Hylæus* F.). Structurally they are the most primitive of all Apoidea as is revealed by the comparatively little modified mouth-parts, the scanty development of the body pubescence and the absence of any special pollen-collecting apparatus. In the Hawaiian Islands Perkins finds that several species are parasitic upon their congeners but the habit appears to be exceptional. Their nests are placed in the stems of bramble and other plants, in the earth, or in chinks in buildings. In these situations they construct cells which are lined by a thin, translucent membrane: the latter serves to retain the honey which is stored in a particularly fluid condition. The family ranges into both hemispheres and is represented in Britain by eleven species.

FAM. COLLETIDÆ.—The genus *Colletes* was formerly placed in the preceding family on account of the short broad sub-triangular ligula. The females bear a resemblance to the workers of the honey bee but the males are considerably smaller. Their general hairiness, larger size and venational differences readily separate them from *Prosopis*. The various species burrow in the soil of sandy localities, sometimes forming extensive colonies. These tunnels are often 10 inches in length, they are lined with a delicate parchment-like membrane, and the cavity of each tunnel is divided by means of partitions of the same substance into about 5 to 8 or 10 cells. An egg is deposited in each cell on, or in, a somewhat fluid mixture of pollen and honey. The family ranges into both hemispheres and several species of *Colletes* occur n Britain.

FAM. ANDRENIDÆ.—An extensive family comprising a large number of moderate or large-sized species which often bear a resemblance to the hive bee. Most of them construct burrows in the ground and frequently in gravel paths, among grass, etc., storing the cells with honey and pollen. Although they are solitary bees they live for the most part in colonies or "villages" which sometimes contain a thousand or more nests. The sexes are very different in appearance, they are not often found together, and are difficult to correlate. *Andrena* is represented in Britain by about 50 species: many of them are double-brooded, occurring in early spring and again n July or August (vide Perkins, *Trans. Ent. Soc.* 1919). In some species the two broods differ slightly from one another, especially with regard to the males. The members of this genus, and also of *Halictus*, are economically important by reason of their pollinating the blossoms of fruit trees. *Halictus* constructs branched tunnels n the ground in very similar places to those selected by *Andrena*. It includes for the most part small bees, certain of its members attaining a length of only 5 mm., and in some species they exhibit metallic coloration. According to Fabre (*Ann. Sci. Nat.*, 1879) *H. lineolatus* and *sexcinctus* exhibit the initial stages of social life. These bees live in colonies and the members thereof collaborate in constructing a common gallery which ramifies in the soil and affords ingress to the various cells. The construction of the latter, however, and the feeding of the brood, is the work of individual bees. According to Verhoeff *H. quadricinctus* builds its cells in a single mass instead of distributing them along the course of the burrow, which is the more usual procedure. The species of *Sphecodes* are small shining black, or black and red, bees with a very rudimentary pollen-collecting apparatus. Their economy has given rise to much discussion but there appears to be little doubt that certain species, at least, are parasites in the nests of *Halictus* and *Andrena*. Both this genus and *Halictus* are well represented in the British Isles. The genus *Andrena* is very subject to parasitism by Strepsiptera, the effects of which may vary considerably among its different species: for an account of these parasites and the morphological changes which they nduce in their affected hosts, vide p. 541.

FAM. PANURGIDÆ.—The members of this small family resemble *Andrena* in habits and construct burrows in sandy or gravelly localities. *Panurgus* is a genus of deep black bees which is represented in Britain by two species.

FAM. STELIDIDÆ.—The members of the genus *Stelis* are black bees with the abdominal terga margined with white. The British species are parasitic on *Osmia* but elsewhere the recorded hosts include *Anthidium*, *Chelostoma*, and *Ceratina*. According to Verhoeff (*Zool. Anz.*, 1892) *Stelis minuta* lays its eggs in the cells of *Osmia leucomelana* and its larvæ consume the food stored therein, sharing it with the legitimate owners. When the provisions are consumed the *Osmia* larva falls a prey to that of *Stelis* and is devoured by the latter.

FAM. MEGACHILIDÆ.—An extensive and almost cosmopolitan family including the leaf-cutting bees and their parasites, together with the mason bees. The genus *Megachile* is well known from its habit of cutting out rounded pieces from the leaves and petals of roses and other plants. Leaf-cutting bees resemble the hive bee in general appearance but have broader heads and are rather more robust. Their nests are formed in the soil, in hollow stems, wood and other situations. The cells are constructed entirely of leaves and are thimble-like in shape : the wall of the thimble is formed of layers of large oval pieces of leaves and the lid, which closes the receptacle, is similarly made up of layers of smaller round pieces. The cutting process is carried out with great neatness and rapidity : the female bee holds on to the leaf with her legs until she has excised a piece of the required shape with her mandibles. Each cell is about half filled with a paste of pollen and nectar and an egg is deposited in it in the usual manner : new cells are added end to end and, as they adhere to one another, a nest consists of one or more strings of these chambers. In India, and other hot countries, many species enter houses and block up every available keyhole or other small aperture with clay and the material of their nests. The various species of *Osmia* exhibit great diversity of instinct in nest-formation, but generally choose hollow places already existing whether they be in wood, stems, mortar, in empty snail shells, Cynipid galls or elsewhere. They are mason bees constructing cells of sand, soil, or clay held together with a glutinous substance : internally the cells are smooth but externally they are rough in conformity with the material used in the construction. Usually about 10 to 20 cells are found in a nest and each is stored with a mixture of pollen and honey. Smith recorded a nest of *Osmia parietina* attached beneath a large stone and composed of 230 cells. *O. tridentata* nests in bramble stems while the very common *O. rufa* will form its nest in almost any convenient hollow, whether it be in the ground or in wood, or it may take advantage of a keyhole, snail shell or other object. For original observations on the habits and instincts of this genus the reader is referred to the works of Fabre. Bees of the genus *Chalicodoma* construct nests of exceptionally solid masonry, often attaching them to large stones. Several species occur in the south of France, one of which, *C. muraria*, has formed the subject of some of Fabre's most detailed observations on instinct. It is a densely hairy insect, larger than the hive bee, and the two sexes are markedly different in colour. The cells are constructed of soil particles mixed with the salivary secretion of the insect and, during the process of nest building, many small pebbles are incorporated and cemented in position with the aid of this mortar-like material. After eight or nine cells have been built, the whole is then plastered over with the same substance, and the completed nest assumes a dome-like form about the size of half an orange. Notwithstanding the great hardness of these nests, their inmates are very much subject to the attacks of such parasites as *Anthrax*, *Leucospis* and *Stelis*. In *Anthidium* (Fig. 571) the males are exceptional among Hymenoptera in being larger than the females, and like *Osmia* the species of this genus take advantage of suitable cavities rather than construct burrows for themselves. Some of the species are known to possess the habit of lining their nests with cottony fibres and hairs, which they strip by means of their mandibles from various plants. The single British species, *A. manicatum* L., chiefly occurs in the southern counties, and within the cottony lining of its nest the cells are made of a delicate membrane which serves to retain the stored honey. Other species have been observed by Fabre to use resin in place of cotton for their lining material.

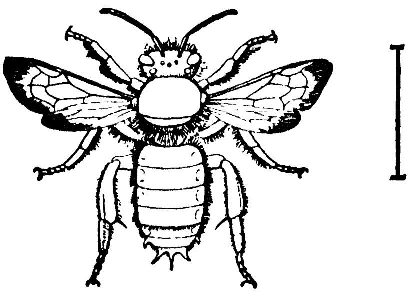


FIG. 571.—*Anthidium manicatum*, Male. Britain.

After F. Smith · reproduced by permission of the Trustees of the British Museum.

Cœlioxys includes a number of bees which are parasites or inquilines in the nests of *Megachile* and *Anthophora*, while *Dioxys* has been bred from the cells of *Chalicodoma* and *Osmia*.

FAM. XYLOCOPIDÆ (Carpenter Bees).—Included in this family are the largest known bees. For the most part they are black or bluish-black with dark, smoky and often iridescent wings : over parts of the body the pubescence is frequently yellow, white, or brown. Although resembling *Bombus* in general appearance they are more flattened and less hairy. Xylocopidæ occur in both hemispheres but are mostly denizens of warm countries : four species are listed by de Gaulle as inhabiting France. These giant bees tunnel by means of their powerful mandibles into the solid wood of beams, rafters, etc., for a foot or more in depth, dividing their burrows into a series of cells made of agglutinated fragments of wood. A single egg is deposited in each cell which is largely provisioned with pollen. *X. violacea* extends as far north as Paris and its habits attracted the attention of Réaumur : both sexes hibernate and reappear the following spring. According to Bingham *X. rufescens* is nocturnal and its loud buzzing may be heard throughout moonlight nights in Burma. In a number of species of these bees, from many parts of the tropics, the basal concavity of the 1st abdominal tergum in the female is provided with a median aperture leading into a large chitinous chamber. The latter appears always to contain Acari belonging to *Greenia* or other genera (vide Perkins, *Ent. Month. Mag.* 1898). The relation between these mites and their hosts has not been fully investigated.

FAM. CERATINIDÆ.—The bees of this family are mostly small, nearly glabrous species, frequently of metallic coloration, and their nests are found in the stems of bramble, elder, and other pithy plants. They are allied to the preceding family and are sometimes known as the small carpenter bees. The British species, *C. cyanea* Kirby, inhabits various localities in the more southern counties.

FAM. NOMADIDÆ.—An interesting family of small and not very hairy insects which live as inquilines in the nests of other bees. Most of the species are wasp-like in coloration and very unlike their hosts whose burrows they frequent without molestation. In accordance with their habits, their legs are not adapted to carry pollen, and their larvæ are fed upon the provisions originally destined for the progeny of the host species. The species of *Nomada* live at the expense of various solitary bees, more particularly *Andrena* ; *Halictus, Eucera* and *Panurgus* are less frequently selected. *Melecta* and *Crocisa* utilize *Anthophora* as their host while *Epeolus* is confined to *Colletes*. According to Ashmead the North American *Epeolus donatus* is not an inquiline, but constructs and provisions cells of its own. Over twenty species of *Nomada* inhabit Britain, and both *Melecta* and *Epeolus* are also represented. An account of the habits of various species of *Nomada* is given by Smith (*Cat. of Brit. Hymenoptera in Coll. Brit. Mus.*) and Perkins (*Trans. Ent. Soc.*, 1919).

FAM. ANTHOPHORIDÆ.—The solitary bees of this family are, for the most part, hairy insects resembling small bumble-bees in form. Many of the species burrow in the soil, constructing cells in underground tunnels, provisioning the former with a mixture of pollen and honey. *Anthophora* is one of the widest distributed genera of bees and much of what is known concerning their economy is due to Friese (1922–23). The large black *Anthophora pilipes* is one of the earliest bees to appear in spring in Britain.

FAM. EUGLOSSIDÆ.—Included in this tropical family are the most remarkable of all bees. *Euglossa* inhabits tropical America and its species are beautiful vividly metallic insects whose ligulæ often exceed the entire length of their bodies. At one time these bees were supposed to be social insects but no workers have been discovered.

FAM. BOMBIDÆ (Bumble or Humble Bees).—The bees of this family include some of the most familiar insects in temperate climates. They are abundant in the holarctic region but generally confined to the mountains in tropical countries. They are absent from almost the whole of Africa, the plains of India and none are indigenous to Australia and New Zealand. The species of *Bombus* exhibit, in temperate regions, a social life which resembles that found in *Vespa* much more closely than that which obtains in the hive bee. The societies come to an end in autumn and a certain number of the females hibernate to reappear in spring when they form new colonies. The most abundant caste is that of the workers but the latter are not clearly distinguishable from the queens or females except by their smaller size. Soon after fertilization the females hibernate and this phase may be passed either in the ground, or in thatch, rubbish, moss, etc. In Britain the period of torpor lasts about nine months and according to Sladen (1912) it may commence as early as July, as is in the case of *Bombus pratorum*. The latter species is astir again in March or April while other species often await until May or even June. Each queen seeks out a situation for her future nest : the latter may be underground and consists of fine grass or moss formed into a hollow ball (Fig. 572). Access to the nest is obtained by means of a tunnel which averages about two feet in length. Other Bombi, known as " carder bees," form surface nests hidden away among grass, ivy or other herbage. They derive their name from their habit of collecting moss and other material used in nest formation and plaiting it with the aid of their legs and mandibles. Having formed the nest the next act of the queen is to collect a mass of pollen which is formed into a paste. Upon the top of this substance she constructs a circular wall of wax and, in the cell thus formed, she lays her first batch of eggs, capping the latter over with a covering of wax. She also constructs a waxen receptacle, or honey pot, which is filled with a store of honey for her own consumption. This store is drawn upon during inclement weather and while the queen is occupied in incubating her eggs. The larvæ hatch in about four days and lie immersed in their food-bed of pollen: the queen further supplies them with regurgitated pollen and nectar which is passed to the brood through a hole which she forms in the upper part of the cell. About the 10th day the larvæ spin tough pale yellow cocoons and on the 22nd or 23rd day after oviposition the first adults appear and are always workers. New cells are added to the nest as the season advances, and each cell contains on an average about a dozen eggs. The workers convert their old cocoons into honey pots and, in some species, additional waxen vessels are also constructed. When sufficient workers have emerged, the work of pollen-collecting devolves upon them and the queen becomes restricted to the nest. After the queen has deposited about 200–400 worker eggs, according to the species, she lays other eggs which give rise to males and queens. Those destined to produce queens are laid in larger cells than is the case with worker or male eggs, the worker cells being the smallest of the three types. Both Huber and Schmiedeknecht state that the male and queen cells are not provisioned before the eggs are laid in them, and those larvæ destined to produce queens do not appear to receive any different diet from those which will give rise to males. During the intermediate period in the life of the colony the females which are produced are smaller than the parent, and are little more than egg-laying workers. The large-sized females, together with the males, do not appear until the end of the season. The survivors among these females form the next year's colonies: the males, on the other hand, are short-lived and having once left the nest do not return to it. The nest of *Bombus* usually presents an irregular appearance: the larvæ, as they develop, increase in size, and their cell becomes distended, and has a mammilated appearance. The queen adds more wax to the covering so that the larvæ always remain hidden, but much of the wax is removed after the cocoons are formed. The cells are only utilized once for rearing purposes and fresh cells are added above the old remains. The members of the genus *Psithyrus* are inquilines in nests of *Bombus*, each species generally sharing the food and shelter of a particular species of host. Furthermore, the colour and size resemblance of the inquiline to the *Bombus* with which it is commonly associated is especially striking. This is very evident in two abundant British Psithyri, i.e.: *P. rupestris* closely resembles *B. lapidarius* and *P. vestalis* likewise closely simulates *B. lucorum*. According to Sladen the above-

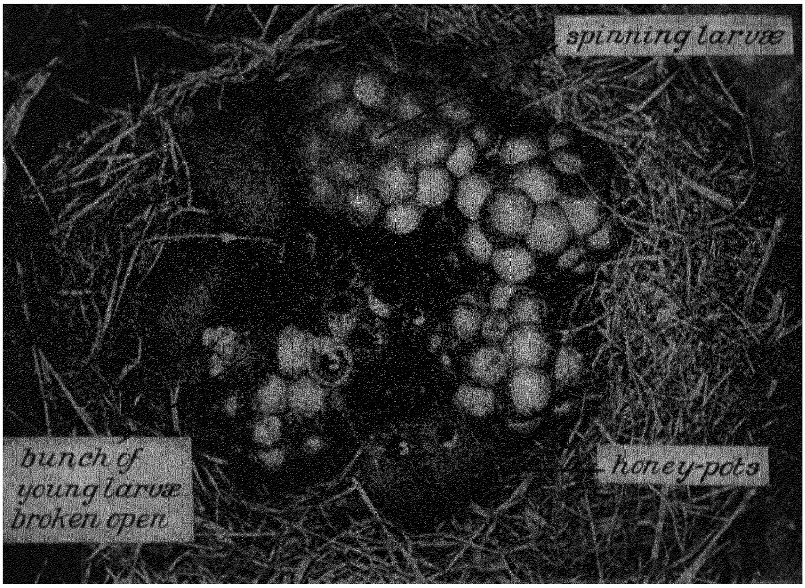


FIG. 572.—NEST OF *BOMBUS LAPIDARIUS*.
After Sladen.

mentioned species of *Psithyrus* sting the *Bombus* queens to death and usurp their places in the nests, the *Bombus* workers rearing the *Psithyrus* offspring. In such affected nests the population of the host species is naturally greatly reduced in numbers. From the nature of its life *Psithyrus* produces no workers and its males and females differ from those of *Bombus* in their more resistant and shinier integument which, in so far as the abdomen is concerned, is less densely clothed with hair. Owing to the absence of any polliniferous apparatus, the outer surface of the hind tibia of the female *Psithyrus* is convex and uniformly hairy, whereas in *Bombus* it is more or less concave, bare and shiny but marginally clothed with long hairs. In *Psithyrus* also, the female lacks both the comb at the apex of the hind tibia and the auricle at the base of the metatarsus.

The number of British species of the family depends upon the specific validity of certain names (Richards, *Trans. Ent. Soc.* 75, 1927). Saunders recognizes fifteen species of *Bombus* and five of *Psithyrus*. The biology of these species is described in the well-illustrated manual of Sladen (1912) : the works of Friese and von Wagner (1910) and Hoffer (1882) are also important.

FAM. APIDÆ.—The best known member of this family is the hive or honey bee, *Apis mellifica*. It has probably been more completely studied than any other species of insect, its habits having attracted attention from very early times. The structure and biology of this insect have been discussed in many volumes dating from the Renaissance onwards, and the details of its economy are so readily accessible that only the more important features will be referred to here. The insect is rarely, if ever, found wild in Britain, and has been introduced into almost every country of the globe. It is usually regarded as the highest member of the Apoidea, and differentiation into the three forms male, female, and worker is more pronounced than among other bees. The male, or drone, is larger and stouter than the worker, and is readily distinguishable from the latter caste by the large holoptic eyes, whose great development is accompanied by a corresponding reduction of the frontal region of the head. The female, or queen, has a particularly long abdomen extending some distance behind the closed wings. She performs none of the functions of nest building, food gathering, or brood care and lacks the special organs adapted for these purposes. Large prosperous colonies have been computed to contain 50,000 to 80,000 workers, besides a queen and a variable number of males. The queen is able to survive for several seasons, but the males and workers are relatively short lived. Summer-hatched workers, owing to continuous toil, seldom appear to survive longer than six or seven weeks, but those hatched in autumn live to perform the labours of early spring. The colonies of this species are, therefore, not merely seasonal but are maintained from year to year, and are stored with provisions for winter consumption. When the population increases beyond the capacity of the hive, swarms are emitted which consist of the queen and a number of workers. In this way the new community is fully prepared for both nest building and reproduction. The original colony is dominated by a new queen and, prior to her emergence, the old queen is prevented from destroying her by the workers. The latter, as far as possible, only allow new queens to develop when it is desirable to emit a swarm. The virgin queen takes what is known as the marriage flight, and is followed by a number of males. Copulation occurs in mid-air and the fertilized queen then returns to the nest. If a second swarm be emitted the same season, a new virgin queen accompanies the workers and, as the swarm usually journeys further from the nest than the previous swarm, an opportunity is afforded for the queen to be fertilized by a male from another colony. At the end of the summer, the workers always eject the males from the hive, since they have no further part to play in the life of the community.

The honeycomb, or structural basis of the nest (Fig. 573) is composed of cells which are mostly hexagonal in form, and arranged in two series, placed back to back. The separate combs hang vertically downwards and the long axes of the cells are almost horizontal. The material used in construction is wax which is secreted by the younger workers. It is a product of hypodermal glands situated on the ventral aspect of the fourth to seventh abdominal sterna. The wax is secreted as a fluid and, according to Dreyling (*Zool. Anz.* 26), it is exuded through extremely fine cuticular pores, subsequently accumulating and hardening in the form of thin plates. The latter project from pockets situated between adjacent sterna, and the bee removes the wax plates by impaling them on the spines of the distal end of the first tarsal joint of the hind-leg (Casteel, *U.S. Entom. Circ.* 161). The leg is then flexed forwards, and the wax seized by the mandibles and kneaded into the required condition to form the cells. The cells in which workers develop are smaller than those destined for rearing the males, while the royal cells in which the queens are produced are the largest of all and irregularly ovoid in form. Other of the cells are devoted to the storing of pollen and honey. In addition to wax, the workers also utilize a resinous substance which they collect from the buds and other portions of various trees. The material is termed propolis, and is used as a kind of glue to fasten loose portions of the comb and to fill up crevices, etc. The queen lays a single egg in each brood cell, and the incubation period is about three days. When the larvæ are fully grown, the workers seal up the cells by means of a cover of wax and pollen: thus enclosed the larvæ form the so-called cocoons in which pupation takes place. The complete development of the queen occupies approximately 15½ days, the worker three weeks, and the male 24 days. The young larvæ are at first uniformly nourished on a diet rich in proteid (40–43 per cent.) which is provided by the workers. Little is known as to the origin of this food but it is usually considered to be a secretion of the lateral pharyngeal glands. The larvæ of the queens are fed upon this diet throughout life, while those destined to produce workers and males are nourished upon honey and digested pollen from the fourth day[1] onwards. The subject of sex-determination is a highly complex one and it may be said that it is generally agreed that the virgin eggs produce the drones and the fertilized eggs the queens and workers. In rare cases, however, workers may produce queens and other workers from unfertilized eggs (Jack: *Trans. Ent. Soc.*, 1916).

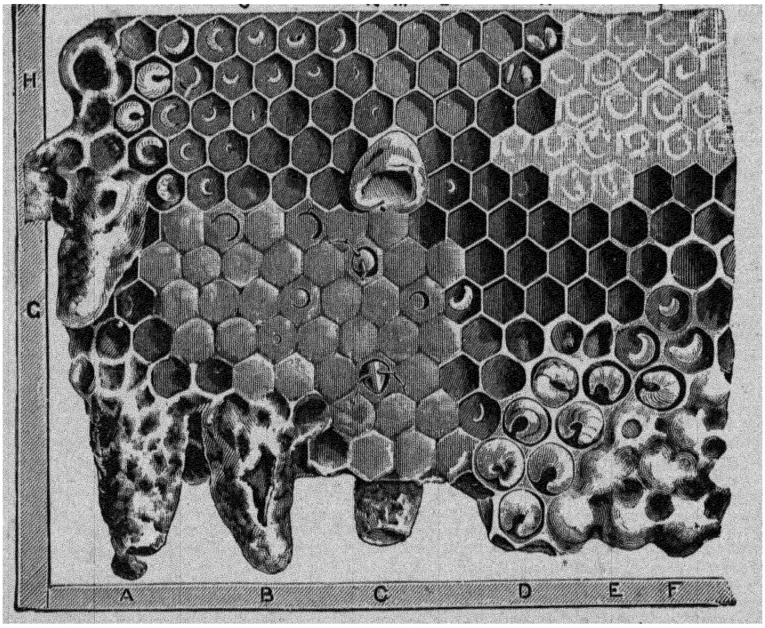


FIG. 573.—COMB OF HIVE BEE (NATURAL SIZE).

A, empty queen cell; *B*, do. torn open; *C*, do, cut down; *D*, drone larva; *E*, *F*, sealed drone cells; *G*, sealed worker-cells; *H*, old queen cell; *I*, sealed honey; *K*, pollen masses; *L*, pollen cells; *M*, abortive queen cell; *N*, emerging bee; *O*, eggs and larvæ. *After* Cheshire.

A variety of flowers are visited by bees in order to gather nectar, the most important being Dutch clover: heather, lime, other clovers, the blossoms of fruit trees and bushes, buckwheat, white mustard, etc., are also largely resorted to. The nectar, when gathered, largely consists of cane sugar which, in its conversion into honey, becomes inverted into glucose and lævulose. In addition to nectar, bees also utilize honey-dew and the juices of over-ripe or damaged fruits. In order to supplement the foregoing account the reader is referred to the work of Snodgrass (1925) for anatomical details, and for general information, including the theory and practice of apiculture, to the writings of Cheshire (1886), Zander (1919–23), Root, Langstroth, and many others: the literary masterpiece of Maeterlinck (1901) should also be mentioned.

The only other species of *Apis* are the three Indian representatives, *A. dorsata*, *indica*, and *florea*. *Apis dorsata* constructs a single huge comb sometimes three or four feet in diameter. It is suspended quite exposed from rocks, branches, or from buildings. This species is easily irritated and readily attacks man or domestic animals, sometimes with fatal results. *Apis indica* is a sub-species of *mellifica* while *A. florea* is the smallest member of the genus and in some respects transitional between *dorsata* and *indica.*

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[1] According to recent work by Nelson and Sturtevant (*Bull.* 1222, *U.S. Dept. Agric.*) the change of diet takes place on the third day.

The genera *Melipona* (Fig. 574) and *Trigona* (vide also p. 545) include about 250 species which are mainly neotropical with a certain number of members found in the tropics of the Old World. They nest in hollows in trees and rocks, or in walls, and their colonies include enormous numbers of often minute individuals (sometimes less than 3 mm. long) known as " mosquito " or " stingless " bees : the latter expression, however, is a misnomer, since a vestigial sting is present (vide von Ihering, 1904). Both males and workers secrete wax which is produced between the abdominal terga : it is usually mixed with earth or resin forming a dark material called " cerumen." The nest consists of a part containing the brood which is separate from that devoted to storing honey and pollen. The entrance to the nest usually projects as a conspicuous funnel which is often guarded by workers during the day and closed with cerumen at night. For the species of *Melipona* and their habits see Schwarz (1932).

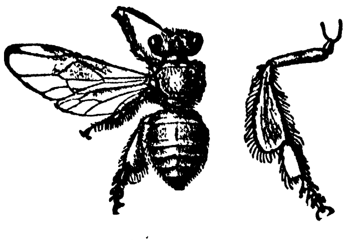

FIG. 574.—*MELIPONA LUTEA* × 2. INDIA.
After Bingham (F.B.I.).

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Order 22. DIPTERA (Two-winged or True Flies).

INSECTS WITH A SINGLE PAIR OF MEMBRANOUS WINGS, THE HIND PAIR MODIFIED INTO HALTERES. MOUTH-PARTS SUCTORIAL, USUALLY FORMING A PROBOSCIS AND SOMETIMES ADAPTED FOR PIERCING: MANDIBLES RARELY PRESENT: LABIUM USUALLY DISTALLY EXPANDED INTO A PAIR OF FLESHY LOBES. PROTHORAX AND METATHORAX SMALL AND FUSED WITH THE LARGE MESOTHORAX: TARSI COMMONLY 5-JOINTED. METAMORPHOSIS COMPLETE, LARVÆ ERUCIFORM AND APODOUS, FREQUENTLY WITH THE HEAD REDUCED AND RETRACTED: TRACHEAL SYSTEM VARIABLE, MOST OFTEN AMPHIPNEUSTIC. PUPA EITHER FREE OR ENCLOSED IN THE HARDENED LARVAL CUTICLE OR PUPARIUM: WING-TRACHEATION REDUCED.

The Diptera are one of the largest orders of insects including about 50,000 described species, and approximately 5200 species are known from the British Isles. Structurally Diptera are among the most highly specialized members of their class. The imagines of almost all the species are diurnal and the majority are either flower-lovers, which feed upon nectar, etc., or frequent decaying organic matter of various kinds. Although these two habits predominate, a considerable number of flies are predaceous and live on various insects which form their prey. In addition to the foregoing, there are other Diptera which have acquired blood-sucking habits, and in addition to man many other vertebrates, excepting fishes, may be resorted to by one or other species. Excluding the Anthomyidæ and Pupipara, this habit is largely confined to the female. The blood-sucking forms include almost the whole of the Culicidæ, besides the Simulidæ, Tabanidæ and Pupipara, also certain members of the Chironomidæ, Psychodidæ and Anthomyidæ. In virtue of this propensity the order has acquired great significance in relation to medical science. The pathogenic organisms of some of the most virulent diseases such as malaria, sleeping sickness, elephantiasis, and yellow fever are transmitted to man through the intermediary of blood-sucking Diptera.

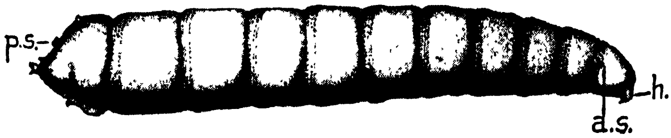

FIG. 575.—A TYPICAL CYCLORRHAPHOUS LARVA (*HYLEMYIA*). *h*, head; *a.s.*, *p.s.*, anterior and posterior spiracles.

External Anatomy

The **Head** (Fig. 576) is remarkable on account of its mobility and is usually of relatively large size. An extensive portion of its area is occupied by the *compound eyes* which, as a rule, are considerably larger in the male than the female. When the eyes of the two sides are contiguous they are stated to be *holoptic*, and when markedly separated *dichoptic*; very occasionally the holoptic condition is found in the female as well as the male.

In some species the upper facets are larger and more conspicuous than the lower, a peculiarity rarely seen in the female. It assumes its most extreme development in the Bibionidæ where the two areas of different facets are sharply defined (Fig. 79). Between or slightly behind the eyes are the *ocelli*: the latter are usually three in number and are generally arranged in the form of a triangle: in some families ocelli are wanting. A complete Y-shaped epicranial suture is present in *Mycetophila* but, as a rule, the anterior arms alone are evident: among Schizophora the epicranial suture is totally wanting (Peterson). The terminology of the regions of the head in general use is confusing owing to the multiplicity of names which have been employed: many do not admit of wide application and are often devoid of morphological value. In a Muscoid fly the " front " [1] is regarded as the region between the eyes, and is limited by a line drawn through the bases of the antennæ and by the upper margin of the head. In holoptic flies the space between the eyes and the basal line of the antennæ is the *frontal triangle*: the triangular region bearing the ocelli and often bounded by grooves or depressions is the *ocellar triangle*. The region enclosed by the frontal suture is the *face* (facial or mesofacial plate) which is demarcated laterally by the *facial ridges* (facialia or vibrissal ridges) and distally by the epistoma. At the lower extremities of the facial ridges are two prominences or *vibrissal angles* carrying the vibrissæ. The antennæ are frequently lodged in *antennal grooves* or foveæ which may be separated by a median *facial carina*. The *genæ* (parafacials or cheeks) comprise the region lying between the face and the anterior margin of the eye on either side, while the *jowls* are the lower portions of the genæ below the eyes. The upward continuations of the genæ, along the inner border of the eyes, are known as the *geno-vertical plates* or *parafrontals*. The *epistoma* is the distal border of the face and, in front of it, is a sclerite which is here regarded as the *clypeus* (or fronto-clypeus). In many Nematocera the fronto-clypeus is a well defined region but in some Brachycera and all Cyclorrhapha the clypeus (tormæ of Peterson) appears to be separated off as a distinct sclerite. The latter is frequently a crescentic or semilunar plate, lying in the membrane of the rostrum, and forming the anterior or dorsal wall of the fulcrum.

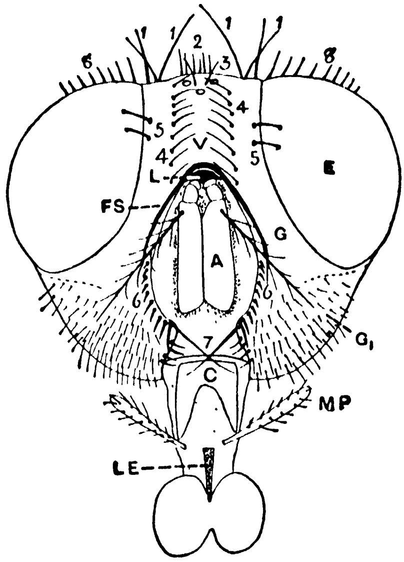

FIG. 576.—FRONTAL VIEW OF HEAD OF A CYCLORRHAPHOUS FLY (SCHIZOPHORA).

A, antenna; *C*, clypeus; *E*, eye; *FS*, frontal suture; *G*, gena and lower portion G_1 or jowl; *L*, lunule; *LE*, labrum-epipharynx; *MP*, maxillary palp; *V*, vertex. The numerals refer to the chætotaxy (p. 624).

The **Ptilinum** or frontal sac is a characteristic cephalic organ of Cyclorrhapha and its presence is indicated externally by the arched *frontal* or *ptilinal suture*. The latter lies transversely above the antennæ and extends downwards on each side of them, thus presenting a ∩-shaped form. The suture is of the nature of an extremely narrow slit, along the margins of which the wall of the head is invaginated to form a membranous sac or ptilinum, and the walls of the latter are seen to consist of the same layers as the integument. The outer surface of the ptilinum is roughened owing to the presence of minute scales or spines of various forms. When viewed in sections taken through the head, the ptilinum is seen lying in the cavity of the latter in front of the brain. Attached to its inner surface in certain positions, are groups of slender muscle-fibres which apparently aid in retracting the organ. The function of the ptilinum is to thrust off the anterior end of the puparium at the time when the contained imago is ready to emerge. This is accomplished by the sac being exserted and distended in front of the head, under pressure from within (Fig. 577). When fully protruded it is in the form of a bladder, which presses upon the wall of the puparium until the latter ruptures. After the emergence of the fly, the ptilinum is withdrawn into the head cavity and is no longer functional. The only outward manifestation of its existence is seen in the presence of the frontal suture. The ptilinum, however, offers a field for investigation both from the developmental and physiological points of view: there is also a great deal of doubt as to its presence or absence in certain families. In the Aschiza the frontal suture is vestigial or absent and no trace of the ptilinum can be detected in the several families. Just above the bases of the antennæ in the Cyclorrhapha is a small crescentic sclerite known as the *frontal lunule*: in the Schizophora it is separated by the frontal suture from the part of the head immediately above.

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[1] In most Diptera almost the whole of the anterior surface of the head appears to be formed by the vertex: the true frons is either of very limited extent or merged with the clypeus.

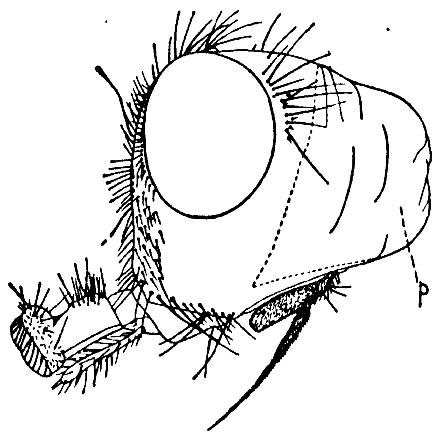

Fig. 577.—Head of *Calliphora* (seen immediately after Emergence from Pupa) with Ptilinum *p* inflated.

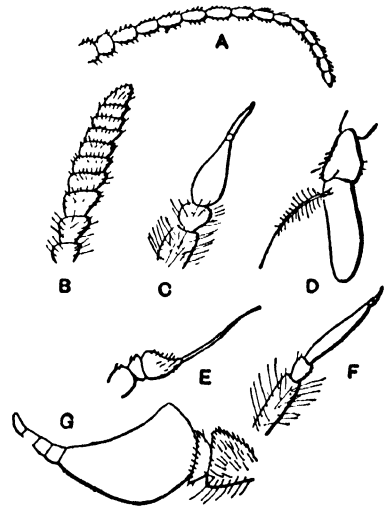

Fig. 578.—Antennæ. *A*, *Mycetophilid*. *B*, *Bibio*. *C*, *Empis*. *D*, *Sarcophaga*. *E*, *Leptis*. *F*, *Bombylius*. *G*, *Tabanus*.

The **Antennæ** (Fig. 578) furnish some of the most important characters in the classification of Diptera. They are seen in the least modified condition among the Nematocera, where the flagellum consists typically of a variable number of cylindrical joints similar to one another. In the Brachycera the antennæ are composed, as a rule, of a smaller number of dissimilar elements. They consist of 2 or 3 evident basal joints carrying a terminal appendage, which corresponds to the greater part of the flagellum in Nematocera. This appendage may be distinctly annulated or jointed, or very much attenuated when it is known as a *style*. If it is still more slender and bristle-like it is termed an *arista*, which is a characteristic feature of the Cyclorrhapha. Morphologically, there is no clearly marked distinction between a style and an arista: the former, however, is always terminal while the latter is usually dorsal and rarely terminal. In the Cyclorrhapha the antennæ similarly consist of three basal joints of which the 3rd is the largest and most complex and carries the arista. The various forms of the arista are of classificatory value, and they may be either bare, plumose, or pectinate.

The **Mouth-parts** of Diptera exhibit a wide range of structure in adaptation to diverse habits, and there are many differences of opinion in interpreting the morphology of certain of the component parts. The generally accepted homologies as presented by Dimmock (1881) are confirmed by Kellogg (*Psyche,* 8) who, from a study of the larval head in Nematocera, observed that the developing imaginal mouth-parts are found in unmistakable correspondence or homologous relations with the larval counterparts. A similar conclusion was arrived at by Miall in his study of the head of *Chironomus.* There is, however, much diversity of opinion with reference to the homologies of the maxillæ and their palpi: thus Meinert (1881) contends that the latter are not the strict homologues of the maxillary palpi of other insects but of the entire maxillæ. Kellogg finds that the palpi in *Simulium* develop in relation with larval maxillæ, and not with their palpi, a fact which lends some support to Meinert's view.

Although the most generalized type of mouth-parts in Diptera is far removed from the orthopterous condition, the following features can be recognized. (1) The *labrum-epipharynx* consisting of a dorsal well-chitinized labrum and a ventral more membranous epipharynx. (2) *Mandibles* are absent except in many of the blood-sucking forms. (3) The *maxillæ* are very rarely if ever complete: the basal sclerites may be separate and distinct, or either the cardo or stipes may be wanting. A single maxillary lobe or galea is generally evident among Orthorrhapha and, in a few genera (e.g. females of *Simulium* and *Tabanus*) a vestigial *lacinia* may also persist. The galea is very variable in development and may be almost filiform (*Exoprosopa*), rod-like (*Sciara, Trichocera*), or totally wanting (*Tipula, Dolichopus*). The maxillary palpi are particularly important for classificatory purposes: they may consist of four complete joints, but in the more highly specialized forms they are reduced to single-jointed organs. (4) The *labium* forms the proboscis which is usually expanded distally to form a pair of prominent fleshy lobes or *labella.* Recently Crampton (1921) has brought forward evidence which suggests that the latter organs are the reduced and modified labial palpi. In most Nematocera the labella are free, but in the higher Diptera coalescence takes place to a greater or lesser degree. With the beginning of coalescence fine trachea-like food channels or *pseudotracheæ* become evident: they attain their most complete development in the Calypteræ where the fusion reaches its maximum. In the majority of Diptera a posterior chitinized plate (*theca*) is present near the base of the labella and is probably the counterpart of the mentum (Fig. 581), while the submentum is represented by the median membranous area behind the theca. (5) The *hypopharynx* is probably universally present and is either in the form of a lanceolate organ or a greatly attenuated stylet. It is perforated by the salivary duct and is frequently considerably developed.

The mouth-parts attain their fullest development in those Nematocera and Brachycera with blood-sucking habits. In these forms the trophi, with the exception of the palpi and labium, are either stylet-like or blade-like, and adapted for piercing. The females, moreover, are unique among Diptera in possessing mandibles. In the males the latter organs are rarely present and are usually atrophied, except in the Simuliidæ and in the group Ceratopogoninæ. The labrum-epipharynx in these blood-sucking forms is grooved or ∩-shaped, and the hypopharynx flattened: when apposed, the two elements constitute a closed channel through which the blood is drawn by the pumping action of the pharynx. The hypopharynx conveys the saliva to the distal orifice of the channel where it mixes with the blood. The wound on the host is made either by the mandibles alone, or in conjunction with the galeæ of the maxillæ. The labium takes no part in piercing: it is grooved dorsally and serves as a sheath retaining the other appendages when at rest (Fig. 579). In the Tabanidæ (Fig. 580) both mandibles and maxillæ are flattened and blade-like, minutely serrated distally: the labrum-epipharynx is shaped like a double-edged sword, and overlies a similar but more slender hypopharynx. In addition to functioning as a sheath for the other mouth-organs, the labium in Tabanids is also an organ for imbibing liquid matter from moist surfaces, which is absorbed by the pseudotracheæ present on the labella. In the Culicidæ (Fig. 579) specialization has been carried a step further, all the mouth-parts are more elongated and the piercing organs are modified into extremely fine needle-like stylets. The labella have many sensory hairs on their distal margins and are mainly tactile in function: the method of feeding in this family is dealt with on p. 643. In the predaceous Brachycera (Asilidæ and Empidæ) the labium is hardened and horny with the labella

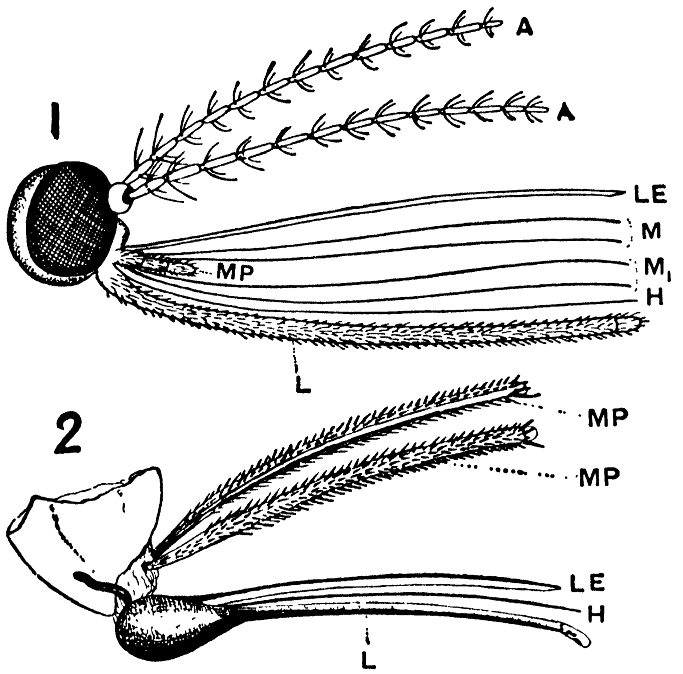

FIG. 579.—MOUTH-PARTS OF 1, *CULEX*; 2, *GLOSSINA PALPALIS*.
A, antenna; *H*, hypopharynx; *L*, labium; *LE*, labrum-epipharynx; *M*, mandibles; M_1, maxillæ and *MP*, palpi; (2 *after* Stephens and Newstead).

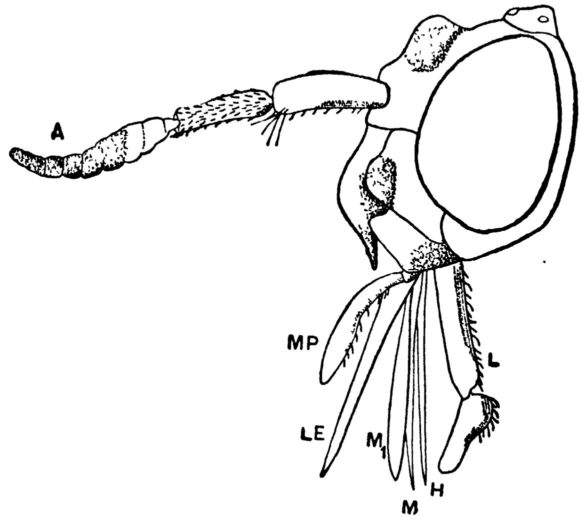

FIG. 580.—*CHRYSOPS*, LATERAL VIEW OF HEAD × 15.
A, antenna; other lettering as in Fig. 579. *After* Surcouf and Gonzalez-Rincones.

small, and usually with poorly developed pseudotracheæ. The galeæ are rigid and blade-like, being seemingly adapted for perforating the prey: both the labrum-epipharynx and hypopharynx are large and strong.

In most Cyclorrhapha all the mouth-organs contribute to the formation of the proboscis. Its morphology is difficult to appreciate owing to the modification which has resulted through the reduction of the maxillæ, and the increased development of membranous areas, in order to impart to the organ the maximum flexibility. The anatomy of the proboscis has been most fully studied in *Calliphora* (Fig. 581). In this genus (Graham-Smith, 1930) it consists of a proximal and somewhat cone-shaped basal portion or *rostrum*, and a distal portion or *haustellum*. Morphologically the rostrum belongs to the head and carries anteriorly the *maxillary palpi*. Situated within this region is a complex framework of chitin known as the *fulcrum*, which forms a kind of case enclosing the pharynx, and is present in almost all Diptera. The proximal portion of the fulcrum is quadrangular in section, and the distal portion U-shaped, the anterior or roof-like portion being wanting in this region. The superficial or anterior portion of the fulcrum is hinged basally to the oral margin. Between the lower end of the fulcrum and the base of the labrum-epipharynx is a small U-shaped

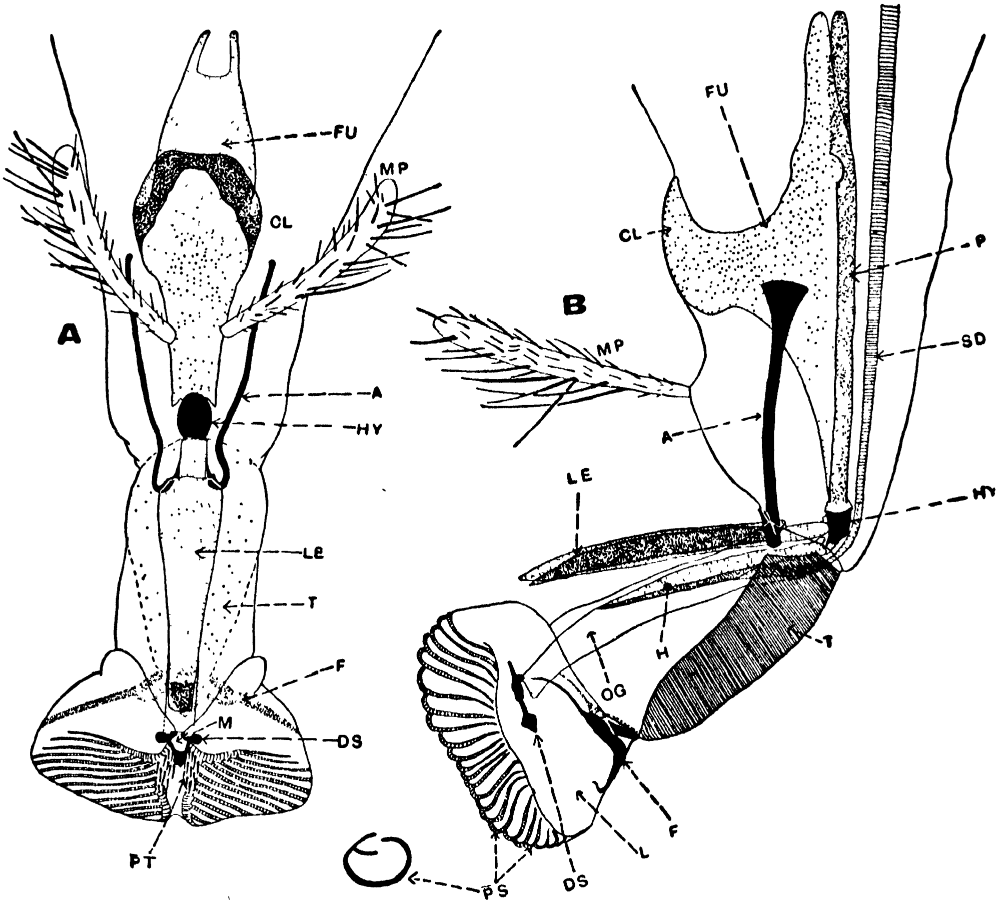

FIG. 581.—PROBOSCIS OF *CALLIPHORA*. A, FRONTAL, B, LATERAL VIEW.

A, apodeme (stipes); *CL*, clypeus; *DS*, discal sclerite; *F*, furca; *FU*, fulcrum; *H*, hypopharynx; *HY*, hyoid sclerite; *L*, labellum; *LE*, labrum-epipharynx; *M*, mouth; *MP*, maxillary palp; *OG*, oral groove; *P*, course of pharynx; *PS*, pseudo-tracheæ; *PT*, peristomial teeth; *SD*, salivary duct; *T*, theca.

hyoid sclerite which lies on the pharyngeal wall, and serves to keep the lumen of the pharynx distended. The haustellum carries the labrum-epipharynx and the hypopharynx on its anterior (or dorsal) face, and these organs are situated in a furrow formed by its projecting membranous sides. The haustellum is continuous with the apex of the rostrum and, on its posterior aspect, it is strengthened by the *theca*. The latter articulates distally with a short rod or *furca*, and arising therefrom are two divergent arms which form the principal skeleton of the oral lobes. The membrane investing the oral or distal surface of the labella contains a series of food channels or *pseudotracheæ* which pass from its outer edges to the inner margins. These channels are kept open by a framework consisting of a series of incomplete chitinous rings which impart to them an appearance resembling tracheæ. Each ring is bifurcate at one end and single at the other—the single and bifurcate extremities alternating. The pseudotracheæ open on the external surface of the oral lobes by means of the spaces which lie between the forked extremities of the chitinous rings : inwardly they communicate with the oral aperture. The latter is situated in a small oral pit between the labella : the sides of the depression are bordered by a row of prestomal teeth which are greatly developed in *Ochromyia* and blood-sucking Muscids. The proboscis is adapted for sucking up liquids, and none but the most minute solid particles are able to enter the food channels. Under certain conditions the labella may be strongly reflected which allows of the protrusion of the prestomal teeth and their use as rasping organs. When this occurs food can be sucked directly through the oral aperture which admits particles of larger size than could traverse the pseudotracheæ. When the proboscis is protruded, the rostrum is extended by means of the distension of the lateral air-sacs at its base, and probably of certain of the cephalic air-sacs also. The haustellum, on the other hand, is brought into use by means of the contraction of its extensor muscles and, finally, the labella are extended and rendered turgid by means of blood-pressure. The retraction of the proboscis is brought about by the contraction of its numerous muscles.

In the blood-sucking Anthomyidæ and the Pupipara the proboscis itself has become modified to form the principal organ of penetration. It differs from that of most Cyclorrhapha in its horny consistency and swollen bulbous base : owing to the elongation of the haustellum the proboscis can no longer be concealed when retracted. In *Stomoxys* the labella are small oval lobes, devoid of pseudotracheæ, and have their outer membrane provided with plate-like chitinous teeth adapted for cutting. The labrum-epipharynx and hypopharynx are shorter than the proboscis and, consequently, do not perform any part in the making of the wound : they have, furthermore, thin and flaccid distal extremities. In *Glossina* (Fig. 579) the proboscis is embraced by the elongate palpi when at rest, and specialization has proceeded still further. The labella are even less evident, and the slender labrum-epipharynx lies throughout in close contact with the labial groove and, for this reason, has lost much of its rigidity. In *Hippobosca*, *Olfersia* and their allies the basal portion of the proboscis is sunk within the head, the distal part of the organ alone being visible. It bears no labella but the cutting teeth exhibit a bi-lateral arrangement. The labrum-epipharynx is much stouter than in the preceding genera and, instead of lying within the labial groove, it forms the roof of the latter. The hypopharynx in *Hippobosca* is a slender flattened organ containing the salivary duct between its two layers : at its upper end the dorsal lamina fuses with the epipharynx and the ventral lamina merges into the lining of the labial groove.

The principal general papers regarding the mouth-parts of Diptera are those of Dimmock (1881), Hansen (1883), Meinert (1881), Kellogg (1899), Peterson (1916), and Frey (1921) : for the Pupipara and *Glossina* the reader is referred to papers by Jobling (1926–33).

The **Tentorium** is characterized by three pairs of arms and a reduced body : the primitive invaginations persist to a greater or less degree in most Diptera as intra-cranial tunnels. As a rule the most prominent invaginations are those of the anterior arms (well seen in *Chironomus* and *Anopheles*) which are situated some distance below the antennæ, and are often located within the arms of the V-shaped suture. The invaginations of the dorsal arms lie just below the bases of the antennæ, but as a rule they are wanting : those of the posterior arms are situated near the ventro-lateral margins of the occiput (Peterson, 1916).

The **Thorax** (Fig. 582) is characterized by the great development of its median segment which carries the wings, and the correlated reduction of the segments in front and behind it. The two latter regions are little more than anterior and posterior bands, whose active function is the support of the fore- and hind-legs. The consolidation of the three segments is so complete, particularly in the higher Diptera, that it is difficult to determine the homologies of the various plates with any degree of certainty. The views that are held on this subject are so divergent, and the terminology so unsettled, that it is only possible to deal with it very briefly in the space available. The sclerites are well exhibited for preliminary study in Tipulidæ, but among Cyclorrhapha real difficulty will be experienced owing to the specialization which has resulted.

The *pronotum* in Tipulids is represented by a band-like scutum and scutellum, but is still more reduced in the higher Diptera. The *mesonotum* forms the greater part of the dorsal aspect of the thorax and is clearly divisible into prescutum, scutum and scutellum : the post-scutellum of this segment is well developed in Tipulidæ, Culicidæ, and other Nematocera, but is narrow among the higher Diptera. The boundary between the prescutum and scutum is known as the *transverse suture* and, although complete and V-shaped in Tipulids, it is generally incomplete in the middle line in other Diptera. On the mesonotum are certain more or less prominent lateral swellings on either side, which are recognized by systematists, and known as calli or callosities. The *pre-alar callus* is situated just above the root of the wing, while the *humeral callus* forms the antero-dorsal angle of the prescutum, and the *post-alar callus* constitutes the prominent postero-dorsal angle of the scutum. The *metanotum* is always reduced and band-like, and is continuous laterally with the epimera.

The pleura do not present any serious difficulties among typical Nematocera and Brachycera, and both episterna and epimera can be recognized in each segment. Among Cyclorrhapha, however, the interpretation of the pleurites is in a far from satisfactory condition, and the extensive use of chætotaxy for classificatory purposes demands the definition of these plates with precision. The terminology of Osten-Sacken, although of limited application, has much to recommend it for the somewhat paradoxical reason that it has no strict morphological value. In cases where homologies are uncertain and extremely difficult to determine, a purely conventional terminology presents more chances of fixity, and can coexist with the growth of a more scientific system, based upon increasing knowledge of comparative morphology. In Osten-Sacken's nomenclature the pleural regions are identified in relation to certain well-defined sutures. (1) The *notopleural suture*, running from the humeral callus to the wing base, thus separating the mesonotum from the pleuron: (2) the *sternopleural suture*, running below the notopleural suture and separating the mesopleura from the sternopleura: (3) the *mesopleural suture*, passing downwards from the wing-base to the middle coxa. The *mesopleuron* is the area in front of the root of the wing between the noto- and sterno-pleural sutures: the *pteropleuron* lies below the root of the wing and behind suture 3: the *sternopleuron* is situated below suture 2 and above the anterior coxa: the *metapleuron* lies behind the pteropleura and to the outside of the metanotum: the *hypopleuron* is the region above the middle and posterior coxæ and below the metapleuron (vide Fig. 582). For further information on the thorax of Diptera vide Snodgrass (1909), Osten-Sacken (1884) and Crampton (1925).

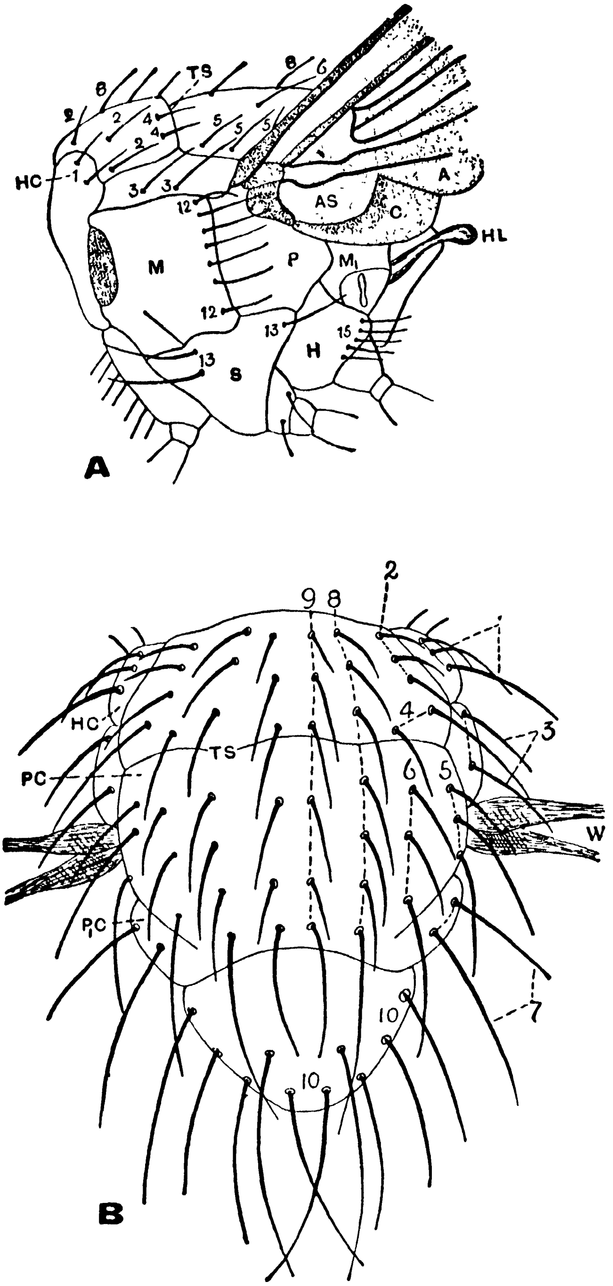

Fig. 582.—Thorax of A, *Lucilia cæsar* × 11; B, *Compsilura concinnata*, dorsal view × 11.

A, alula; *AS*, antisquama; *C*, calyptra; *H*, hypopleuron; *HC*, humeral callus; *HL*, haltere; *M*, mesopleuron; M_1, metapleuron; *P*, pteropleuron; *PC*, pre-alar callus; P_1C, post-alar callus; *S*, sternopleuron; *TS*, transverse suture; *W*, wing-base. The numerals refer to the chætotaxy, vide p. 625. Adapted from Surcouf and Gonzalez-Rincones.

Chætotaxy.—The study of the arrangement of the *macrochætæ* or differentiated bristles of flies is termed by Osten-Sacken *chætotaxy*. His important paper (1884) emphasized the value of these structures for classificatory purposes, and their application has been greatly extended by more recent writers, notably Girschner. A knowledge of chætotaxy is essential for the systematic study of Diptera and the following are the most important of the macrochætæ (Figs. 576, 582).

A. CEPHALIC BRISTLES.—1. *Vertical:* inner and outer pairs situated close to and rather behind the upper inner corner of the eye. 2. *Postvertical:* just behind the ocelli. 3. *Ocellar:* one pair in the ocellar triangle. 4. *Frontal:* a double row in front of the ocelli, external to the frontal suture, often descending to the base of the antennæ. 5. *Fronto-orbital:* one or more on each side of the front near the orbit, behind 4, and immediately below 1. 6. *Facial:* a series above 7, on either side of the face external to the antennæ. 7. *Vibrissæ:* stout, placed close to the sides of the epistoma. 8. *Post-orbital:* a row nearly parallel with the posterior margin of the eye.

B. THORACIC BRISTLES. 1. *Humeral:* one or more on the humeral callus. 2. *Posthumeral:* near the inner edge of the humeral callus. 3. *Notopleural:* one pair between the humeral callus and the base of the wing. 4. *Presutural:* one or more immediately in front of the transverse suture on either side. 5. *Supra-alar:* between 3 and 7, above the root of the wing. 6. *Intra-alar:* several between 5 and 8. 7. *Post-alar:* behind 5, on post-alar cellus. 8. *Dorso-central:* a row on either side of 9, on the inner part of the mesonotum. 9. *Acrostichal:* a row along each side of median line. 10. *Scutellar:* along the margin of the scutellum.

C. LATERAL THORACIC BRISTLES. 11. *Propleural:* immediately above coxæ of fore-legs. 12. *Mesopleural:* on the mesopleura. 13. *Sternopleural:* on the mesosternum. 14. *Metapleural* (trichostichal): on the metapleura. 15. *Hypopleural:* on the hypopleura.

D. ABDOMINAL BRISTLES. 1. *Marginal:* inserted dorsally on the margins of the segments (Tachinidæ). 2. *Discal:* one or more pairs near the middle of the segments. 3. *Lateral:* one or more near the lateral margins of the segments.

The **Legs** do not call for any detailed mention and, except in a few abnormal forms, the tarsi are 5-jointed. In many Acalypteræ a differentiated bristle is present on the outer border of the tibiæ, a short distance below the apex, and quite distinct from the tibial spurs. It is known as the *preapical bristle* and considerable importance has been ascribed to it for classificatory purposes. For the same reason the pads of the feet are noteworthy: thus, pulvilli may be wanting or vestigial in many Nematocera, or may be replaced by a single pad-like arolium (Scatopsinæ). In the Stratiomyidæ, Tabanidæ, etc., both the pulvilli and the arolium are pad-like, while among the Asilidæ there is a stiff and bristle-like empodium. Two pad-like pulvilli are the rule among Cyclorrhaphæ.

Wings are usually present but are wanting or vestigial in a certain number of forms. Apterous or sub-apterous species are principally found in maritime and insular genera (Clunioninæ, Ephydridæ, etc.), parasites (Pupipara), and among species inhabiting ant's and termite's nests (Phoridæ, *Termitomastus*). Occasional apterous species, not associated with the above modes of life, occur in various families, notably *Chionea, Epidapus* (female) and certain Borboridæ.

The venation of the more generalized members of the order shows a tolerably close approximation to the hypothetical primitive type, the chief differences being the atrophy of Cu_2 and the vestigial condition of 2A and 3A. Neither accessory nor intercalary veins are developed, and only the chief cross-veins are present. A very primitive dipterous wing is seen in the Tipulid *Protoplasa* which exhibits all four branches of Rs and M, while there is no tendency towards the apical coalescence of adjacent veins. It has been pointed out by Comstock that in all Nematocera, in which Rs is 3-branched, R_2 and R_3 remain distinct: while in those Brachycera that have Rs 3-branched (Fig. 584) R_4 and R_5 are separate. Among certain other of the Brachycera Rs is 2-branched only, and this condition obtains among the Cyclorrhapha. According to Tillyard Cu_1 of Comstock is in reality M_4, while its basal section is Comstock's *m-cu* cross-vein. The lettering of the venational figures is in accordance with this interpretation.

On the posterior margin of the wing, near the base, there is frequently a free lobe or *alula*, and on the inner side of the latter there are often one or two additional lobes or *squamæ* (erroneously termed tegulæ). When two squamæ are present, the one nearest the alula is known as the *antisquama* (antitegula), the squama being the lobe nearest the thorax (Fig. 582). In the Calypteræ the squama is large, usually covering the haltere, and is often referred to as the *calyptron* (or calypter). All three lobes are well seen in *Musca* and *Calliphora*.

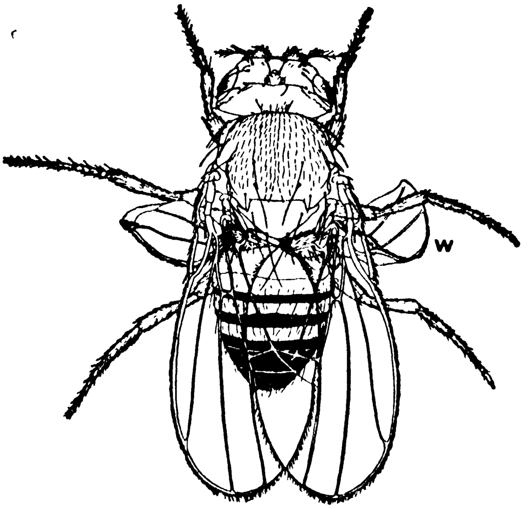

FIG. 583.—*Drosophila melanogaster*: Mutant with Halteres replaced by Hind Wings *W*.

After T. H. Morgan, *Publ. Carnegie Inst.* 327, 1923.

With the exception of a few degenerate apterous forms (ex. *Melophagus*, *Braula*, etc.), *halteres* (balancers) are universally present among Diptera. They develop from the dorsal metathoracic wing-buds, and are consequently the highly modified counterparts of the posterior wings. Further proof of their alary origin is also afforded by certain mutations described by Morgan in *Drosophila* in one of which the halteres are replaced by hind-wings with clearly recognizable venation (Fig. 583). Each haltere consists of a dilated basal portion or *scabellum*, which supports a delicate *pedicel* or stalk, surmounted by a knob-like extremity or *capitellum*. The scabellum articulates freely with the metathorax, and is moved by four muscles arising from its proximal border (Lowne): the halteres are, therefore, freely movable and are capable of vibration. It is in the scabellum that the principal sensory structures of the haltere are located. These consist in *Calliphora* of three groups of minute so-called chordotonal organs invested by a thin integument, and three highly sculptured elevations of the cuticle containing larger and more complex structures—the two *scapal organs* (scalæ of Lowne)

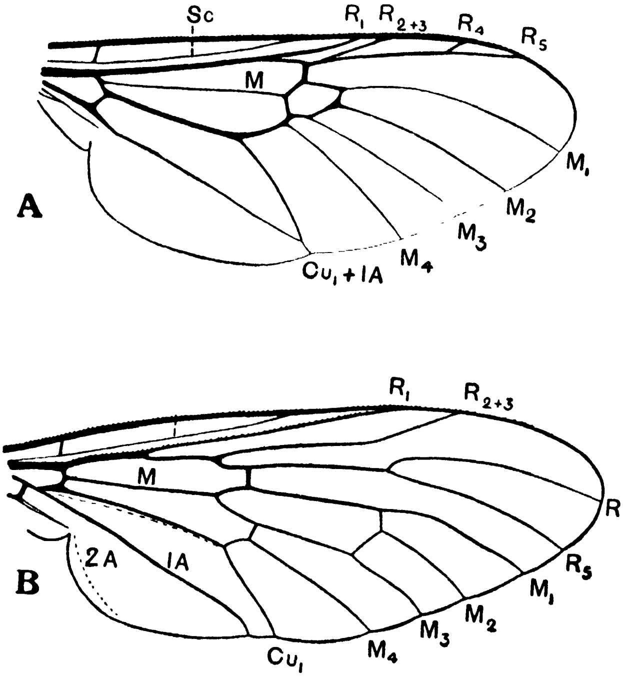

FIG. 584.—Venation of Brachycera. A, *Sargus*; B, *Leptis*.

and the *basal organ* (cupola of Lowne). Both scapal and basal organs exhibit thin transparent areas, each of which overlies a minute vesicle enclosing a central refractive spot. The cavity of the haltere contains blood and a fine tracheal branch. The nerve supplying this appendage is the largest in the thorax. Binet (1894) has demonstrated that the majority of its fibres arise from the brain, and traverse the thoracic ganglia on their course to the metathoracic centre; from there they pass onwards to the scabellum, and are distributed to the several sense organs (vide Lowne, 1890, and Weinland, 1890). Very diverse views have been held with regard to the function of the halteres (Jousset de Bellesme, 1878). They are usually regarded as static organs receiving sensations enabling the insect to co-ordinate its movements during flight: it is likely also that they are capable of appreciating sound vibrations. Experiments conducted with certain species show that, if the capitellum and part of the pedicel of a haltere be amputated, flight becomes clumsy and difficult: if both halteres be treated alike the power of flight is almost entirely lost, and insects so mutilated can only fly a few centimetres, and usually fall vertically when thrown into the air.

In the **Abdomen** the first segment is usually atrophied and the second much reduced. Of the segments that follow the 3rd–11th are present in *Tipula*, but among the Cyclorrhapha the number is difficult to ascertain, and rarely more than 4 or 5 are evident without dissection. In *Dacus* Miyake (1919) finds 11 segments present in both sexes, the 1st segment being represented by its reduced sternum. In the female *Musca* the visible segments are the 3rd to the 6th, while the 7th to 10th segments form the retractile ovipositor. The latter organ is formed in this manner in the majority of Diptera, but in the Tipulidæ a valvular ovipositor is present (Snodgrass, 1897). In the male the 9th and 10th segments are curved ventrally forming the *hypopygium* which may undergo a twist through 180°, or more, in various families. This results in the relations of the parts being inverted or displaced, with the anus often below the ædeagus and the 9th sternum may be dorsal to the tergum (Lamb, 1922). The claspers consist of a large basal sclerite and a movable distal piece, while the ædeagus and its accessory structures lie between the 9th and 10th sterna (vide Edwards, *Ann. Trop. Med. and Parasit.* 1920).

Internal Anatomy

The **Alimentary Canal** is generally but little convoluted among Nematocera, but is more coiled among Brachycera. In the Cyclorrhapha it exhibits greater complexity, its length being much increased mainly owing to the greater extension of the mid-intestine (Fig. 109).

The *buccal cavity* and *pharynx*, or the latter alone, form the sucking apparatus by means of which the food is drawn up through the proboscis and passed into the œsophagus. The original circular lumen in these parts becomes modified, and the chitinous lining is developed as two or three hardened plates. The latter afford a basis for the attachment of dilator muscles, and are capable of being drawn apart by their contractions. In this manner the lumen is increased, and the food sucked up through the siphon formed by the mouth parts. In *Tabanus* both buccal and pharyngeal pumps are present, but in *Bombylius* the pharynx alone performs the suctorial function. Similarly in *Eristalis, Musca* and other Cyclorrhapha, the chief pumping agents are the dilator pharyngeal muscles, the buccal cavity only functioning as a conducting chamber. In Culicidæ the buccal cavity is provided with dilator muscles but the principal pumping apparatus, or pharynx, differs from that of other Diptera in being situated behind the brain. The blood is first pumped into the buccal cavity and from thence it passes into the pharynx, a valve situated between these two regions precluding a return flow.

The *œsophagus* passes through the neck into the thorax where it divides. One branch enters the proventriculus and the other is continued backwards as the slender duct of the food reservoir. The *proventriculus* is the homologue of the gizzard and has a well marked musculature: it never contains denticles and a valve is usually present. The proventriculus is wanting in *Phlebotomus*, *Simulium* and *Culicoides*, is elongate and tubular in *Tabanus* and in *Cyclorrhapha* it is much reduced and disc-like, mainly consisting of its valvular portion. The *food-reservoir* (or crop) is the most characteristic feature of the digestive canal. It is situated in the anterior region of the abdomen and is, morphologically, a diverticulum of the œsophagus. Although present in most families it is wanting in certain Asilidæ, Œstridæ and in *Hippobosca* and *Melophagus*. In *Musca* it is a bilobed sac with very thin walls composed of a single layer of small flattened cells, external to which is a network of muscle fibres; internally it is lined by a delicate cuticle. The usual position of the food reservoir and its duct is ventral, but in *Tabanus* these parts are dorsal. In the Culicidæ, instead of a single sac, three œsophageal diverticula are present, of which two are dorso-lateral, while a third and larger sac is ventral. The function of the food reservoir is that of a storage chamber into which the nutriment is passed as it is sucked up: its contents then become gradually emptied into the mid-gut. The time the food remains in the reservoir varies greatly: thus in *Musca* it may not be emptied for several days, while in *Tabanus* it is usually empty and possibly its contents are quickly regurgitated into the mid-gut (Patton and Cragg). As a rule, after a meal the reservoir is distended with food, as has been demonstrated by allowing flies to feed upon a coloured liquid.

The *mid-intestine* in Nematocera is a pyriform or fusiform sac: in the Culicidæ its anterior region, or cardia, is elongate and tubular, and leads into a dilated chamber or stomach. Among Cyclorrhapha the mid-gut is no longer dilated but is tubular throughout, and thrown into numerous convolutions. It is divisible into an anterior region—the *ventriculus* or *chyle stomach*, followed by a narrower and much longer *proximal intestine*. The *Malpighian tubes* are generally four in number: in most Cyclorrhapha they arise in pairs from a common duct on either side. *Psychoda* and the Culicidæ are exceptional in possessing five Malpighian tubes: in *Culicoides* there are only two (Bugnion).

The *hind-intestine* is divisible into the *distal intestine* and *rectum*. The former, in many Diptera, is naturally separable into a narrow coiled *ileum* and a wider region or *colon*. The rectum is a pyriform or rounded chamber provided with a variable number of papillæ which may be either two (*Chironomus*), four (*Musca*, *Calliphora*, etc.), or six (*Anopheles* and *Tabanus*).

The **Salivary Glands** are usually elongate and tubular but exhibit great variation in length. In the Culicidæ they are situated in the thorax and each gland is trilobed: a layer of secretory cells surrounds the cavity of each lobe, and the smaller central lobe (formerly known as the poison gland) differs somewhat in histological features. The common salivary duct passes to the base of the hypopharynx, where it expels the secretion down the salivary groove to the apex of that organ. In the Tabanidæ the glands extend into the anterior part of the abdomen, while in *Musca* they are considerably longer than the total length of the body.

Labial Glands are frequently present on the proboscis at the bases of the labella. In *Musca* they are spherical aggregations of gland cells. According to Hewitt (1914) the ducts are intra-cellular, each arising from a vacuole. They pass outwards from the gland to form a number of larger ducts which unite and open into the oral pit by means of a pair of median pores. The secretion of the labial glands serves to moisten the surface of the labella.

The **Nervous System** (Brandt, 1879, Kunckel d'Herculais, 1879) presents many modifications, almost every transition being found between the Nematocera, with 3 thoracic and 7 abdominal ganglia, and the Calypteræ in which all of the ganglia of the ventral chain are fused into a single thoracic mass (Fig. 65). There is, furthermore, a marked relation between the degree of concentration of the nervous system and specialization in other directions. A graduated series illustrating the progressive concentration of the nervous system may be exemplified as follows.

1. Two or three thoracic centres and always six abdominal centres: 1st abdominal ganglion united with the metathoracic and the 7th and 8th abdominal ganglia fused (most Nematocera also Asilidæ, Empidæ, Bombylidæ and *Xylophagus*). 2. Three thoracic and five abdominal centres (Scenopinidæ). 3. Two thoracic and four abdominal centres (Therevidæ). 4. Two thoracic and no abdominal centres (Dolichopodidæ). 5. One thoracic and five abdominal centres (Tabanidæ, Stratiomyidæ). 6. One thoracic and two abdominal centres (Syrphidæ). 7. One thoracic and one abdominal centre (Conopidæ and most Acalypteræ). 8. A single thoracic centre (Calypteræ and Pupipara).

In the Nematocera, and also the Leptidæ and Asilidæ, the nervous system of the imagines exhibits only a slightly greater concentration than in their larvæ. Stratiomyidæ, Syrphidæ, Conopidæ and certain Acalypteræ exhibit decentralization in the imago compared with the larva. In the Calypteræ and Pupipara the concentration of the larval nervous system is persistent in the imago. In *Musca* and other Calypteræ the nervous system exhibits the highest stage of concentration. The brain and infra-œsophageal ganglion are closely united to form a compact mass perforated by a foramen for the œsophagus. The thoracic and abdominal ganglia are intimately fused to form a common ganglionic mass situated in the thorax. Posteriorly, the nervous system is prolonged as a median abdominal nerve giving off lateral segmental nerves, two pairs in the thorax, and the remainder in the abdomen (Fig. 65D).

In the **Female Reproductive System** there is a variable number of polytrophic ovarioles (Fig. 585). The latter are fewest in number in larviparous species: thus in *Glossina, Musca bezzi* and *Termitoxenia*, a single ovariole is present on each side, while in *Melophagus* and *Hippobosca* there are two. The majority of Diptera, however, are oviparous and the ovarioles are much more numerous, their number varying from about 5 to over 100. In *Chironomus* the morphology of the ovaries is peculiar: each consists of a central axis radiating out from which is a large number of short ovarioles, the whole being enclosed in a delicate membrane (Miall and Hammond).

Spermathecæ are universally present: they are usually conspicuous dark brown or black globular sacs, lined with chitin. There may be a single spermatheca present (*Anopheles, Simulium*), or two (*Mansonia, Phlebotomus, Dacus*), or three (*Culex, Stegomyia*, the Tabanids and most

Calypteræ). A pair of tubular accessory glands is usually present opening into the dorsal region of the vagina. Small and unpaired in *Anopheles*, they are large in Tabanids, elongate and filiform in *Musca, Hypoderma*, and most other Calypteræ. Their normal function apparently is to secrete a viscid substance which enables the eggs to adhere to one another or to the substratum upon which they are laid. In *Glossina* and the Pupipara they secrete a milky fluid which serves to nourish the intra-uterine larva.

Viviparity is not infrequent among Calypteræ and is of general occurrence in the Pupipara: among other Diptera it is exceedingly rare but occurs in *Chironomus stercorarius*. Viviparous Diptera may be divided into two main groups as follows (Keilin 1916):—

GROUP I.—Species whose larvæ hatch from the eggs in the uterus of the parent but exhibit no special adaptations to an intra-uterine life. Included in this group are numerous Tachinidæ which produce a large number of minute eggs and the larvæ emerge within the uterus which is greatly elongated for their reception. In some species the larvæ hatch outside the parent, immediately after the eggs have been laid. Larviparity is characteristic of the Sarcophaginæ, but in this group the eggs are larger and fewer: usually 40 to 80 are produced at a time and the larvæ are deposited in their first instar. In a number of other species (*Theria muscaria, Mesembrina meridiana, Hylemyia strigosa, Musca larvipara, Dasyphora pratorum*, etc.) a single very large egg is produced at a time and the parental uterus is enlarged to form an incubatory pouch. In these instances the larva is retained for a variable time within the parent before deposition and the extreme condition is afforded by *Dasyphora pratorum* in which it has attained its 3rd instar at the time of extrusion.

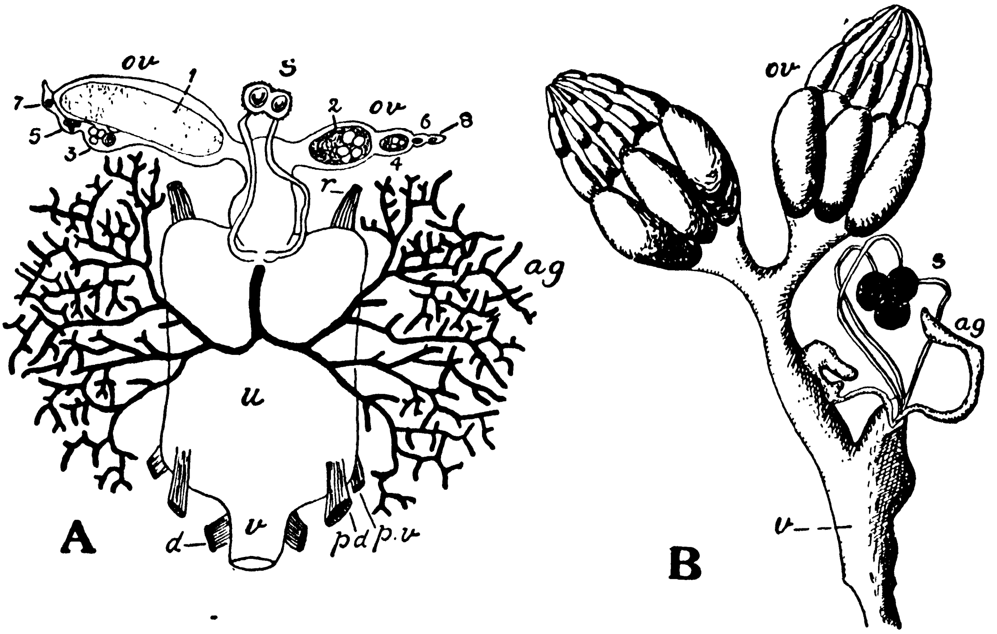

FIG. 585.—FEMALE REPRODUCTIVE ORGANS. A, *GLOSSINA PALPALIS*, ADAPTED FROM ROUBAUD, 1908; B, *MELANOCHELIA RIPARIA* AFTER KEILIN, 1917.

ag, accessory glands; *d*, dilator muscle of vagina *v*; *pd*, *pv*, dorsal and ventral protractor muscles of uterus, *u*; *r*, retractors of same; *ov*, ovary; *s*, spermatheca. The numerals in A refer to the relative ages of the oocytes.

GROUP II includes *Glossina* and the Pupipara. The larva lies in the uterus of the parent and is nourished by the product of special nutritive glands. The secretion is discharged at the apex of a papilla and absorbed directly through the mouth of the larva. The following special adaptations to an intra-uterine life are exhibited. The buccal apparatus is reduced to a single basal sclerite: the mid-gut is a closed sac which does not communicate with the hind intestine and, moreover, is greatly elongated to form a food reservoir; there are no salivary glands. The hind intestine is greatly shortened and forms a receptacle for the accumulation of waste products excreted by the Malpighian tubes. The larvæ when deposited are mature and shortly afterwards pupate.

In the **Male Reproductive System** (Keuchenius, 1913) the *testes* are, as a rule, ovoid or pyriform and frequently pigmented. The vasa deferentia are generally short and become confluent distally to form a common ejaculatory duct. In association with the latter, in many Diptera, is a muscular *ejaculatory sac* probably concerned with regulating the discharge of the seminal fluid. Paired accessory glands are often present.

In *Chironomus*, *Phlebotomus* and *Tabanus* the first portion of the common genital canal is enlarged and functions as a *vesicula seminalis* from which a narrow ejaculatory duct leads to the ædeagus; in these genera accessory glands are wanting. In *Culex* each vas deferens enlarges distally to form a vesicula seminalis, and two pyriform accessory glands open into a very short ejaculatory duct. In *Musca* there are no accessory glands and the ejaculatory duct is a long winding canal: *Calliphora* (Fig. 160) resembles *Musca* but differs in the presence of accessory glands. In *Dacus* the latter consist of about 16 blind tubuli (Miyake, 1919), while in *Hypoderma* there is a small unpaired globular gland. In the Pupipara the genital organs attain their greatest complexity, and the testes are in the form of compactly coiled tubuli resembling balls of thread. The reproductive organs of *Glossina* resemble those of Pupipara rather than of Anthomyidæ, the testes being similar densely coiled tubes. The ejaculatory sac is an organ of variable structure: in *Musca* it contains a chitinous, phylliform *ejaculatory apodeme* which aids in propelling the seminal fluid along the genital canal during copulation (Hewitt). In *Dacus* the ejaculatory sac is very large, while in *Phlebotomus* its place appears to be taken by an organ termed by Grassi the "pompetta"—a piston-like chamber provided with a movable rod: since the opening of the ductus ejaculatorius is near the lower end of this chamber, the latter is believed to regulate the seminal flow after the manner of a pump.

The **Heart** has been very little investigated: in *Musca* (Hewitt) and *Calliphora* (Lowne) it is divided into four large chambers, corresponding to the visible abdominal segments, and a small anterior chamber: each chamber in *Musca* has a pair of dorso-lateral ostia at its posterior end. Anteriorly the heart is prolonged as a tube of narrow calibre.

The most important feature of the **Tracheal System** is the great development of air-sacs, particularly among Cyclorrhapha. In *Musca* and *Volucella* the air-sacs occupy more space than any other organs, and the hæmocœle is consequently much reduced. The largest and most prominent of the air-sacs are the abdominal: numerous sacs are also present in the thorax and head (Hewitt, 1914; Kunckel d'Herculais, 1879).

Literature. General works on the anatomy of adult Diptera are extremely few: a good deal of information will be found in the writings of Dufour (1851) and the text-book of Patton and Cragg (1913). For the detailed structure of individual types vide Miall and Hammond (1900) for *Chironomus*; Nuttall and Shipley (1901–03) for *Anopheles*; Kunckel d'Herculais (1879) for *Volucella*; Hewitt (1914) for *Musca*; Lowne (1890) foi *Calliphora*; Tulloch (1906) for *Stomoxys*; Cragg (1912) for *Hæmatopota*; and Roubaud (1909) for *Glossina*

Metamorphoses

No other order of insects presents so great a diversity of larval habits as the Diptera. Four families only have the great majority of their species phytophagous in the larval state, i.e. Cecidomyidæ, Trypaneidæ, Agromyzidæ and Oscinidæ, while the Mycetophilidæ and Platypezidæ are fungivorous. The saprophagous habit is largely in evidence among the Anthomyidæ. Other notable scavengers are the Bibionidæ, Sepsidæ, Phoridæ, Helomyzidæ and Cordyluridæ. True parasitism, either internal or external, obtains in the Tachinidæ, Œstridæ, Pipunculidæ, Conopidæ, Bombyliidæ, Cyrtidæ and Nemestrinidæ. Next to the parasitic Hymenoptera, the Diptera constitute the most important natural controlling agency over the increase of other insects. The predaceous habit occurs in many families, particularly among the Brachycera, and in numerous members of the Syrphidæ, Muscidæ, and Anthomyidæ. With the exception of many Sciomyzidæ and Ephydridæ, the truly aquatic larvæ belong mostly to the Nematocera and to the Stratiomyidæ and Tabanidæ among the Brachycera.

In their larval instars many Diptera affect the operations of man or his person. The four phytophagous families enumerated above include some of the most serious pests the agriculturist and fruit grower have to contend with. The larvæ of the pear and wheat midges, of the Mediterranean fruit fly, the frit and gout flies are cases in point. Among the Anthomyidæ, the larvæ of the cabbage root fly and onion fly bring about great losses to growers of those vegetables.

The science of parasitology is concerned with many dipterous larvæ which directly affect the bodies of man and domestic animals. Under the term *myiasis* are included all affections produced by dipterous larvæ among vertebrates, and more particularly mammals. The species concerned are either parasitic or saprophagous, and it is frequently possible to distinguish between primary myiasis, which is induced by true parasites, and secondary myiasis which is brought about by saprophagous larvæ. The latter only follows on diseased conditions, wounds, and usually where there is microbic infection.

From the clinical standpoint myiasis in man may be grouped as follows:—

1. CUTANEOUS MYIASIS : the larvæ primarily concerned are those of *Dermatobia*, *Cordylobia* and *Bengalia*. Species of *Hypoderma* and *Gastrophilus* also occasionally induce myiasis. 2. MYIASIS OF THE CRANIAL CAVITIES (orbital, nasal, and auditory) : caused by larvæ of *Œstrus*, *Rhinœstrus*, *Gastrophilus* and *Dermatobia*. When of a secondary nature it is commonly due to larvæ of *Sarcophaga*, *Musca*, or *Chrysomyia* : auditory myiasis appears to be always of a secondary nature and follows some purulent affection of the ear. 3. MYIASIS OF THE DIGESTIVE CANAL : larvæ of at least 18 genera have occurred in the alimentary tract, but probably many pass through without causing recognizable symptoms.

In almost all cases of human myiasis the occurrence of dipterous larvæ is occasional, and their presence is a departure from their normal host or mode of life.

Dipterous *larvæ* (Fig. 575) are devoid of true legs, locomotion often either taking place by means of pseudopods, or by the aid of groups of shagreen-like spinules, frequently located on swellings of the body-wall. The greatest number of undoubted segments present is twelve, e.g. three thoracic and nine abdominal. Departures from this generalized condition are not infrequent : thus in some larvæ the number is less than twelve, atrophy or fusion of one or more of the somites having taken place. In larvæ possessing more than twelve apparent segments (Rhyphidæ and Therevidæ) two explanations have been offered. Either certain segments have undergone secondary division, or the intersegments have become greatly enlarged so as to assume the appearance of true segments. Keilin (1915) has shown that six groups of sensory organs are present in all Dipterous larvæ, and are in direct relation with the imaginal leg-buds, thus occupying the positions of the ancestral thoracic limbs.

The number of families in which a well developed *head* is present is small; it is fully formed in the Culicidæ, which are described as being "eucephalous," as well as in most other Nematocerous larvæ (except Cecidomyidæ and Tipulidæ). At the opposite extreme, is the so-called "acephalous" condition present in the Cyclorrhapha, where the head is vestigial (Fig. 575). Many dipterous larvæ (e.g. Brachycera) are in a "hemicephalous" or intermediate condition, a reduced head or "jaw-capsule" being present. This type of head is incomplete posteriorly and can be withdrawn into the thorax. A similar condition is found in the Tipulidæ, the skin of the neck being attached to the middle region of the head with the result that the latter is incomplete posteriorly, and permanently imbedded within the body.

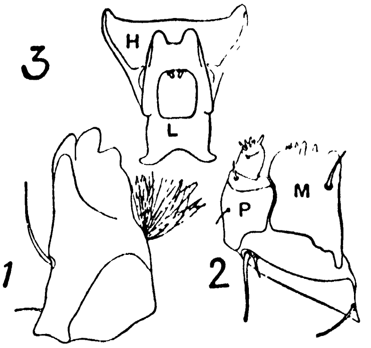

FIG. 586.—MOUTH-PARTS OF LARVA OF *BIBIO MARCI.*

1, mandible; 2, maxilla; *P*, palp; *M*, mala. 3, *L*, labium; *H*, hypopharynx. *After* Morris.

The *antennæ* are variously formed, very rarely prominent, and are composed of 1 to 6 joints. They are best developed in active larvæ which need to seek out their food (Nematocera). In the Mycetophilidæ, many Brachycera and most Cyclorrhapha they are reduced to the condition of small papillæ.

The *mouth-parts* are variable in character in different groups and are exhibited in their least modified condition in certain families of Nematocera. Thus, in *Bibio* (Fig. 586) there is a definite labrum, mandibles are well developed and move in the horizontal plane and the maxillæ are represented by a single lobe or mala and an evident palpus on either side. The labium is in the form of a median plate with a strongly chitinized hypopharynx lying above it on the pharyngeal aspect: labial palpi are wanting. Among the Brachycera the same parts, although variously modified, are more or less evident but the mandibles, on the other hand, work in the vertical plane. In the Cyclorrhapha the typical mouth-parts have undergone atrophy in correlation with the reduction of the head: the maxillæ and labium are scarcely recognizable other than by the papillæ representing their palpi. In this group of Diptera there is a very characteristic framework of articulated sclerites, the whole being known as the *cephalopharyngeal skeleton* (Fig. 587). This structure is a secondary development and is composed of the following principal sclerites. The most anterior are the *mouth-hooks* or *mandibular sclerites* which articulate basally with the hypostomal or *intermediate sclerite.* The latter is H-shaped, its halves being joined by a transverse bar: the hypostomal sclerite receives the opening of the salivary duct. Behind this sclerite is the much larger *basal* or *pharyngeal sclerite.* The latter is formed of two lateral, vertical lamellæ which unite ventrally forming a trough in which is lodged the pharynx.

In many species a chitinous arc (*dentate sclerite*) unites the bases of the mandibular sclerites: various other small accessory sclerites are frequently present, notably in carnivorous species.

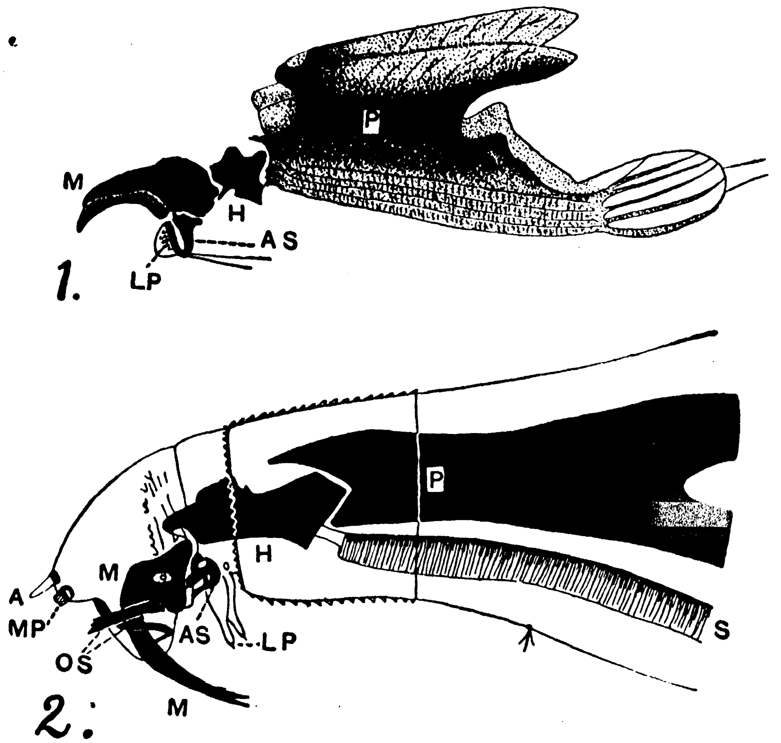

Fig. 587.—Cephalo-pharyngeal Skeleton of Larvæ of 1, *Musca domestica* and 2, *Melanochelia riparia*.

A, antenna; *AS*, dentate sclerite; *H*, hypostomal sclerite; *LP*, labial palp; *M*, mandibular sclerites; *MP*, maxillary palp; *OS*, accessory oral sclerites; *P*, pharyngeal sclerite; *S*, salivary duct. Adapted from Keilin, *Parasitology*, 9, 1917.

Keilin has shown that in saprophagous larvæ the floor of the pharyngeal sclerite is beset with longitudinal ridges which project into the cavity of the pharynx: larvæ feeding on living animal or vegetable tissues are devoid of pharyngeal ridges or, if the latter be present (as in *Pegomyia*) they are reduced (Fig. 588). Furthermore, in phytophagous larvæ the mandibular sclerites are usually toothed, and in carnivorous larvæ they are sharply pointed: in the parasitic forms the buccal armature undergoes marked reduction.

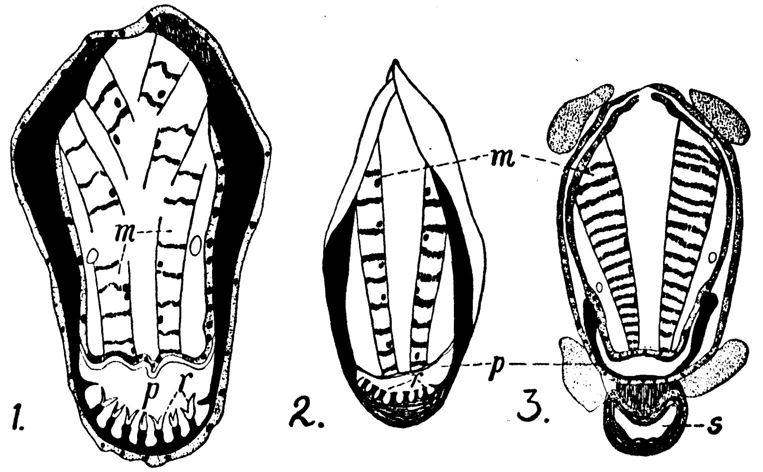

Fig. 588.—Transverse Sections of the Pharynx of Dipterous Larvæ. 1, *Muscina assimilis* (saprophagous). 2, *Pegomyia nigritarsis* (phytophagous). 3, *Syrphus ribesii* (carnivorous).

m, dilator muscles; *p*, cavity of pharynx; *r*, ridges; *s*, salivary duct. *After* Keilin, 1915.

The profound changes which have led to the reduction of the head and the atrophy of the normal biting mouthparts in the larvæ of the Cyclorrhapha appear to be correlated with the two series of factors. Firstly, degeneration consequent upon a life passed in the immediate proximity of an abundance of food, and also a change in the manner of feeding. Secondly, to the backward shifting of the brain and the development of the imaginal head within the larval metathorax. For a general discussion of the head and its modifications among Dipterous larvæ, and the structure of the mouth-parts, the student is referred to the writings of Holmgren (1904), Becker (1910), de Meijere (1916) and Keilin (1915).

Although Dipterous larvæ are apodous in the true sense of the term, pseudopods are present in numerous genera. Thus in *Chironomus*, *Orphnephila* and *Simulium* a pair is present on the prothoracic and anal segments. In *Dicranota* five pairs are evident on segments 6 to 10: in *Eristalis* there are 7 pairs while in *Atherix* and *Clinocera* there are 8. Circlets of pseudopods are present in the abdominal region in *Laphria* and the Tabanidæ.

The *tracheal system* presents features of great systematic value and the most prevalent type is the amphipneustic one (Fig. 589). The primitive or peripneustic condition is almost entirely confined to Nematocera: the maximum number of pairs of spiracles present is 10 (*Bibio*) while 9 pairs occur in Scatopsinæ, Cecidomyidæ and a few others. Indications of a former peripneustic condition are seen in other forms in the presence of solid stigmatic cords leading from spiracular scars to adjacent tracheæ. The larvæ of Cyclorrhapha, when newly hatched, are metapneustic, becoming amphipneustic in the 2nd and 3rd instars. Among the Aschiza, the prothoracic spiracles in some genera are apparently non-functional, the tracheal system being physiologically metapneustic. The propneustic condition is extremely rare but is stated to obtain in *Polylepta*. Apneustic larvæ are found in *Chaoborus*, in Chironomidæ, and also in *Ceroplatus* and *Atherix*.

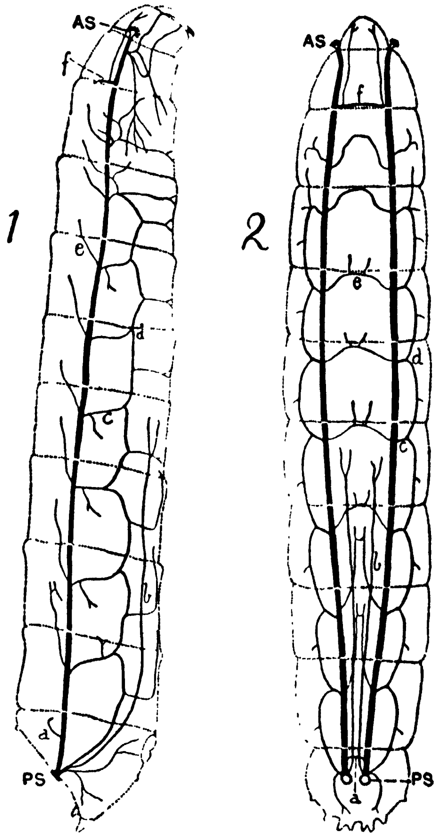

FIG. 589.—AMPHIPNEUSTIC TRACHEAL SYSTEM OF 3RD INSTAR LARVA OF *HYLEMYIA* (ANTHOMYIDÆ).

1, Lateral; 2, Dorsal View. *AS*, anterior spiracle; *PS*, posterior do.

In peri- and amphi-pneustic larvæ the 1st pair of spiracles is carried on the prothorax: in the former condition the 2nd pair is borne on the metathorax or 1st abdominal segment, never on the mesothorax. The segmental position of the posterior pair of spiracles is variable: it is frequently on the last segment whether it be the 11th, as in many Brachycera, or the 12th segment, as in *Dicranota*, *Ptychoptera*, and numerous Cyclorrhapha. In the Culicidæ and certain Brachycera the spiracles are situated on the penultimate segment, and in the Therevidæ and Scenopinidæ on the ante-penultimate segment. In certain metapneustic larvæ (Culicidæ, *Dixa*, *Psychoda*, some Tipulidæ, etc.) the two main tracheal trunks give off a plexus of fine tracheal branches in the neighbourhood of the spiracles, and pass to the walls of the posterior region of the heart. These branches are very thin walled, and it appears probable that the blood is brought into close contact with the oxygen contained therein, and in this way they function as a kind of lung (Imms, 1907).

Accessory respiratory organs in the form of gills are found among aquatic larvæ. In certain Chironomids two pairs of blood gills are situated on the 11th segment, and a similar number of smaller blood gills are present around the anus. Tracheal gills are much more frequent than blood gills: they may be ventral as in the two pairs on the last segment of *Dicranota,* segmental as in *Phalacrocera,* caudal as in Culicidæ, or rectal as in *Simulium* and *Eristalis.* The caudal retractile processes of *Pedicia* and other aquatic Tipulid larvæ are probably of a similar nature.

The *alimentary canal* in larvæ of the Nematocera, and certain Brachycera, is a short tube but little convoluted. In most Cyclorrhapha (Guyenot, 1907) it is greatly lengthened and complexly coiled upon itself. The œsophagus is prolonged backwards into the mid-gut to form an œsophageal valve, or cardia, of varying complexity. In many Cyclorrhapha a food reservoir is present as in the adult. The usual number of Malpighian tubes is four, which may arise separately from the hind-gut, as in *Tabanus* and *Stomoxys.* In *Musca* and most other Cyclorrhapha they unite basally in pairs, each pair communicating with the hind-gut by means of a short duct. In the Culicidæ, *Psychoda, Ptychoptera,* and the Blepharoceridæ five Malpighian tubes are present.

Salivary glands are found in all dipterous larvæ and generally take the form of hollow vesicles lined with a single layer of cells. *Mandibular glands* occur in *Sciara* and extend almost the whole length of the body (Keilin, 1913). Metamerically arranged *hypodermal glands* are found in Tipulid larvæ (Fig. 148), and small *peristigmatic glands* are found in association with the spiracles of many dipterous larvæ.

The *heart* consists of a series of eight chambers in *Anopheles* and other Nematocera. In species of *Chironomus* it is formed of a single enlarged chamber situated in the 11th segment and provided with two pairs of ostia. In *Musca* it comprises three chambers situated in the terminal segments, while in *Dicranota* no distinct chambers are evident (Miall). In all cases the heart is prolonged through the thorax as the aorta, which terminates in the head near the brain. A short distance behind the latter it is surrounded and supported by a collar of irregular cell-tissue—the *cardiac ring* ("anneau de soutien" of Pantel), which is generally present throughout the order.

The *nervous system* in Nematocerous larvæ (Brandt, 1882; Brauer, 1883) consists of the usual supra- and infra-œsophageal ganglia and, as a rule, 3 thoracic and 8 abdominal ganglia. Among the Brachycera this generalized condition of 11 post-cephalic ganglia is present in the Leptidæ, Asilidæ, Therevidæ, and Dolichopodidæ. The Tabanidæ are intermediate between these families and the Cyclorrhapha, reduction and concentration resulting in only 1 thoracic and 5 abdominal ganglia being present. In *Stratiomyia* all the ganglia are fused into a single ovoid ganglionic mass and a similar condition is the rule throughout the Cyclorrhapha (Fig. 144). The position of the brain varies among Nematocera; although usually present in the head as in *Culex,* in *Tipula* and *Ptychoptera* it is situated partially in the head and prothorax, while in *Dicranota, Psychoda* and certain Chironomidæ it lies wholly in the prothorax. In *Calliphora* and other Cyclorrhapha it is situated in the metathorax.

The **Pupa.**—Dipterous larvæ, as a general rule, cast their skins three times during growth, and pupation takes place by one of two methods. In the Nematocera and Brachycera the skin is normally cast at pupation but in the Stratiomyidæ the exuviæ persist and loosely enclose the pupa. In the Cyclorrhapha the pupa is coarctate ; the larval skin hardens forming an outer shell or puparium which encloses the pupa within. The puparium is ovoid or barrel-shaped and quite immobile (Fig. 204). A pupal shelter is formed in several Nematocerous families and among the Brachycera a cocoon is present in certain Dolichopodidæ. Among Cyclorrhapha it is very rare but is found in a few genera of Anthomyidæ. In the lower Diptera prothoracic and 7 pairs of abdominal spiracles are usually evident ; aquatic Nematocera, however, are propneustic. In the puparia of the Cyclorrhapha remains of the larval spiracles can be seen. In *Musca* communication with the air is maintained by means of a pair of pupal spiracles in the form of small spine-like projections between the 5th and 6th segments of the puparium (Hewitt). Similar, though more prominent, respiratory structures are prevalent in other Cyclorrhapha.

Literature on the Larval and Pupal Stages. The only general work on Dipterous larvæ is that of Brauer (1883). Information dealing with the metamorphoses of the Nematocera and Brachycera is given by Malloch (1917), whose paper is accompanied by useful family keys. Verrall's work (1909) contains an account of the larvæ of the Brachycera (by Sharp), while Perris' paper (1870), though old, contains a good deal of information concerning various species. Aquatic Dipterous larvæ have been frequently studied, notably by Meinert (1886), Miall (1895), Grünberg (1910), and Johannsen (1903–95). For the larvæ of Cyclorrhapha the student is referred to Banks (1912) and the writings of Keilin (1915, 1917). Information on the internal anatomy of Dipterous larvæ is extremely scattered : among the more important morphological papers are those of Brandt (1882), Becker 1910), Guyenot (1907), Holmgren (1904), Keilin (1915, 1917), De Meijere 1916) and Vaney (1902).

Classification of Diptera

The Diptera may be classified into three sub-orders, viz. the Nematocera, Brachycera and Cyclorrhapha. The first mentioned include the most primitive forms, the Cyclorrhapha comprise the most highly specialized while the Brachycera occupy a position intermediate between these two groups. In the time-honoured classification of Brauer two sub-orders are recognized, viz. the Orthorrhapha (including the Nematocera and Brachycera) and the Cyclorrhapha. In the Orthorrhapha the imago emerges from the pupal cuticle by means of a dorsal T-shaped longitudinal dehiscence. Among the Cyclorrhapha emergence takes place by an annular dehiscence at the anterior end of the puparium, thus pushing off a kind of cap or lid. There are certain ambiguities in Brauer's scheme and he subsequently modified his views with the result that it is not clear whether his term " orthorrhaphous " applies to the larval or pupal integument or both. In any case the Orthorrhapha, as understood by Brauer, are not a very natural group since the Brachycera are more closely related, as regards the venation, to the Cyclorrhapha than to the Nematocera. The intermediate position of the Brachycera is best expressed by its recognition as a distinct sub-order. The characters of the sub-orders are as given below.

Sub-order I. **Nematocera**

Larvæ with a well-developed exserted head and horizontally biting mandibles; pupa free. Antennæ of imago many jointed, longer than the head and thorax, the majority of the joints usually alike; arista wanting. Palpi usually 4 or 5-jointed, pendulous. Discal cell generally absent, cubital cell when present widely open.

Sub-order II. **Brachycera**

Larvæ with an incomplete head, usually retractile, and with vertically biting mandibles; pupa free. Antennæ of imago shorter than the thorax, very variable, generally 3-jointed with the last elongate; arista or style when present terminal. Palpi porrect, 1 or 2-jointed. Discal cell almost always present, cubital cell contracted before the wing margin or closed.

Sub-order III. **Cyclorrhapha**

Larva with a vestigial head: pupa coarctate. Antennæ of imago 3-jointed with an arista usually dorsal in position. Palpi 1-jointed. Discal cell almost always present. Cubital cell contracted or closed. Head with a frontal lunule and usually a ptilinum (absent in sub-orders I and II).

Literature.—The only general text-book on Diptera is that of Williston (1908), and Wingate's analytical tables (1906) constitute the only comprehensive paper on British species. References to the more important literature on the latter are given by Grimshaw (1917). The more advanced student will find the work of Schiner (1862–64) and Kertesz' catalogue of the palæarctic species (1903–05) indispensable. The latter author has also issued a catalogue of the Diptera of the world (1902) but it has not been completed; the work of Aldrich (1905) contains a useful bibliography of the order. Brunetti's volume (1912) will serve as an introduction to the Nematocera; for the Brachycera Verrall's standard work (1909) is the best introduction and includes most of the British families, while Lundbeck's treatise on the Danish forms is also of great value to the English student. Among Cyclorrhapha, for the British Aschiza see Verrall (1901); for the Calypteræ, the series of papers by Brauer (1897–99), and Brauer and Bergenstamm (1899–05) are important, also those of Girschner (1893), Stein (1916), Séguy (1923), and Townsend (1908, etc.). The work of Lindner (1924–), still in course of publication, deals with all families of palæarctic Diptera.

Sub-order I. **Nematocera**

A certain number of members of this section exhibit exceptional morphological characters. Thus, among the Culicidæ the palpi are stiff and projecting, not pendulous as in other families. When the antennæ are short, and apparently only annulated (Simuliidæ and Bibionidæ), the widened cubital cell and pendulous palpi indicate their affinities with this sub-order. When the palpi are 1 or 2-jointed (certain Cecidomyidæ) the antennal and venational characters remove all doubts.

The following key will serve for the identification of the families :—

1 (4).—Discal cell (1st M_2) present.[1]
2 (3).—Thorax with V-shaped suture on mesonotum. TIPULIDÆ (p. 639)
3 (2).—V-shaped suture absent. RHYPHIDÆ (p. 651)
4 (1).—Discal cell absent.
5 (6).—Small moth-like flies, body and wings clothed with coarse hairs. PSYCHODIDÆ (p. 640)
6 (5).—Not as above.
7 (10).—Wings with network of vein-like creases.
8 (9).—Mouth-parts and true venation absent. DEUTEROPHLEBIIDÆ (p. 650)
9 (8).—Mouth-parts and true venation present. BLEPHAROCERIDÆ (p. 650)
10 (7).—Wings without such network.
11 (12).—Scales present on the wings: usually with slender piercing proboscis. CULICIDÆ (p. 641)
12 (11).—Not as above.
13 (18).—Antennæ shorter than thorax.
14 (15).—Antennæ apparently 2-jointed with a terminal style: anterior wing-veins not markedly thickened. THAUMALEIDÆ (p. 650)
15 (14).—Antennæ many-jointed, with no terminal style: anterior wing-veins more strongly developed than posterior.
16 (17).—Ocelli large: mandibles wanting. BIBIONIDÆ (p. 648)
17 (16).—Ocelli absent: mandibles present. SIMULIIDÆ (p. 649)
18 (13).—Antennæ longer than thorax.
19 (20).—Antennæ terminating in a filamentous prolongation: wing with 10 veins extending to margin. DIXIDÆ (p. 641)
20 (19).—Antennæ without such prolongation: wing with fewer than 10 veins extending to margin.
21 (22).—Wing-veins very few: anal vein absent. CECIDOMYIDÆ (p. 645)
22 (21).—Wing-veins not greatly reduced: anal vein, or vestige, present.
23 (24).—Tibiæ without spurs: coxæ not elongate: ocelli absent. CHIRONOMIDÆ (p. 644)
24 (23).—Tibiæ spurred: coxæ elongate: ocelli present. MYCETOPHILIDÆ (p. 647)

FAM. TIPULIDÆ (Daddy-long-legs or Crane Flies).—ANTENNÆ LONG, 6- TO MANY-OINTED, OCELLI WANTING. LEGS ALWAYS LONG AND FRAGILE, MESONOTUM USUALLY WITH V-SHAPED TRANSVERSE SUTURE, DISCAL CELL PRESENT. OVIPOSITOR VALVULAR, HORNY. LARVÆ METAPNEUSTIC, ANAL EXTREMITY WITH FLESHY RETRACTILE PROCESSES.

The Tipulidæ include some of the largest species of Nematocera. The number of antennal joints is extremely variable and they are occasionally pectinate or serrate n the male, but not plumose. The front of the head is prolonged forwards to a greater or lesser degree, and in a few genera an elongate proboscis is present: throughout he family ocelli are absent. The V-shaped mesonotal suture separates the family rom other Nematocera: in the Ptychopterinæ, however, it is indistinct, and it is wanting in the apterous genus *Chionea*.

The larvæ are usually hemicephalous, the head being deeply imbedded in the prohorax and incomplete posteriorly: in *Ptychoptera* and its allies it is exserted and ucephalous as in most other Nematocera. The antennæ are well developed, the labium is large and toothed anteriorly, and there is usually a large and heavily chitinized hypopharynx. The body is elongate-cylindrical, either with or without pseudopods, 11 or 12-segmented, and usually ashy grey or brownish in colour. Frequently the first 6 abdominal segments are subdivided and, as a rule, the anal segment is truncated, and bears the spiracles. Around the latter is a series of fleshy retractile processes; in aquatic species these processes are often fringed with hairs and protrusible blood-gills are present. In the terrestrial forms the hair fringes and gills are usually greatly reduced. The pupæ are very elongate, and the thoracic respiratory horns are either slender or plate-like.

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[1] Except in *Mycetobia*.

The larvæ of *Tipula* may be taken as representative of the family, and live among grass, roots, etc., decaying vegetation, or are aquatic (vide Brown 1910, Bodenheimer 1924). The larva of *Dicranota* lives in the beds of ponds and streams where it preys upon the worm *Tubifex*. It is characterized by paired retractile pseudopods on segments 6–10, and on the 12th segment there are 3 pairs of outgrowths of the nature of gills (Miall, 1893). The larva of *Ctenophora* and its anatomy has been studied by Anthon (*Journ. Morph.*, 1908) and that of *Holorusia* by Kellogg (1901): descriptions of the larvæ and pupæ of many other genera are given by Malloch (1917) and Alexander (1920).

Larvæ of the Ptychopterinæ (Miall, 1895) are found in damp situations, usually in muddy water where they feed upon the vegetable matter contained therein. They are long and slender with well developed pseudopods armed with spinules: the spiracles are minute, and are borne at the apex of an extremely slender tube formed by the greatly prolonged terminal segments of the body. The pupal respiratory organs are unequal in length, one being many times longer than the other.

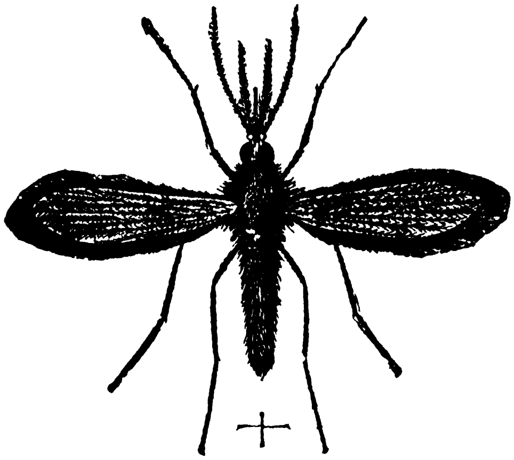

FIG. 590.—*PHLEBOTOMUS SP.*, FEMALE, SUDAN. × 12.

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The larvæ of the Cylindrotomina group are very remarkable: they are green in colour, and aquatic or terrestrial, feeding upon mosses or Angiosperms. The body is provided either with filaments or leaf-like outgrowths: Miall and Shelford (1897) have made a detailed study of the larva of *Phalacrocera* which is aquatic, feeding upon mosses, and the whole body is invested with numerous elongate filamentous processes. In *Cylindrotoma* (Cameron, *Ann. Ent. Soc. Am.*, 1918) the larva is terrestrial with lateral plate-like outgrowths: it feeds openly like a caterpillar on various phanerogamic plants, and the pupa is attached to the food-plant by means of the partially cast exuviæ. Among the Limnobiinæ the larvæ of *Limnobia* are fungivorous, while those of *Dicranomyia* are mostly aquatic or semi-aquatic. A single species of the latter genus is exceptional in having a leaf-mining larva in the Hawaiian Islands.

FAM. PSYCHODIDÆ (Moth-flies, Sand-flies).—MINUTE MOTH-LIKE FLIES, THE LEGS, BODY AND WINGS CLOTHED WITH LONG COARSE HAIRS, OFTEN ADMIXED WITH SCALES. NO OCELLI; WINGS WITH MANY LONGITUDINAL VEINS AND NO OBVIOUS CROSS-VEINS. LARVÆ USUALLY AQUATIC OR SAPROPHAGOUS, OF VARIABLE STRUCTURE, GENERALLY AMPHIPNEUSTIC.

These fragile insects are to be found in close proximity to the larval habitat and are commonly met with in dark or shaded damp situations; some are frequent on windows and are often attracted to a light at night. Females of the genus *Phlebotomus* (Fig. 590) feed by sucking the blood of vertebrates and in some species the male has this habit also. In addition to man, reptiles are used as hosts; and in the case of *P. minutus* lizards and geckos are probably the principal animals preyed upon. The well known "Pappataci" or "three-day" fever was proved in 1908 by Doerr, in Herzegovina, to be carried by *P. papatasi*; possibly other species of the genus also function as carriers. The disease is prevalent in S. Europe, N. Africa, and apparently varieties of the same occur in India. Townsend has brought forward evidence indicating that the disease known as Verruga in Peru is transmitted by another species of *Phlebotomus*. The eggs in this genus are elongate and dark brown; the larvæ have mostly been found in damp, dark places such as crevices in rocks and stone walls, in drains, unclean cellars, moist earth, etc. Their minute size, however, renders them extremely difficult to discover and further information is greatly needed with reference to their habitat. When fully grown the larva is about 2 mm. long, and provided with elongate caudal bristles which may be almost as long as the body. Decaying vegetable matter appears to be their chief food. The pupa is found in similar situations and usually carries the larval exuviæ at its anal extremity. For further information on this genus reference should be made to papers by Grassi (1907), Newstead (1911) and Larrouse (1920).

The Psychodinæ have very doubtfully been accused of the blood-sucking habit which, at any rate, is extremely rare in this sub-family. Their larvæ possess a well developed head and 12 trunk segments, the first and last carrying a pair of spiracles (vide Dell, 1905, Malloch, 1917, and Miall and Walker, 1895). The last segment is drawn out and provided with 4 fleshy outgrowths clothed with elongate hairs. By this means it forms a kind of siphon surrounding the posterior spiracles, and is protruded to the surface of the water. The thoracic and 1st abdominal segments are transversely divided, the remaining abdominal segments being triannulate. Dorsally, the larva carries a series of strongly chitinized plates bearing sensory hairs. These plates are present on each segment (*Pericoma*) or only on the posterior segments (*Psychoda*). The larvæ are aquatic, or live in fluid organic matter of various kinds, including sewage filter-beds. Those of *Ulomyia* and *Maruina* live in cascades. In the latter genus they are provided with ventral sucker discs as in Blepharocerid larvæ, and moreover are metapneustic (Müller, 1895). The larvæ of *Trichomyia* lives in decaying wood (Keilin, 1914). It is narrowly cylindrical, smooth, and devoid of dorsal plates and setæ; the segments are undivided, and the tracheal system is amphipneustic with no respiratory siphon. In the remarkable genus *Termitomastus* Silv., found in the nests of neotropical termites, the wings are reduced to strap-like rudiments: two other termitophilous genera, *Termitodipteron* Holmg. and *Termitadelphos* Holmg., occur in the nests of *Eutermes* in Peru.

FAM. DIXIDÆ.—INSECTS ALMOST DEVOID OF HAIRS AND SCALES, ANTENNÆ ELONGATE, ABOUT 16-JOINTED, FILIFORM APICALLY. VENATION AS IN CULICIDÆ; PROBOSCIS SOMEWHAT PROJECTING, NOT ADAPTED FOR PIERCING: OCELLI ABSENT. LARVÆ METAPNEUSTIC AND AQUATIC, USUALLY ASSUMING A U-SHAPED ATTITUDE.

A very small family comprising the genus *Dixa* which is largely holarctic and includes about two dozen species. These insects have been variously included in the Culicidæ and Tipulidæ. They are readily separable from most of the latter by the absence of the discal cell and the V-shaped thoracic suture: the filiform non-plumose antennæ are totally different from those organs in the Culicidæ, and find their parallel in *Trichocera*. They closely resemble the Culicidæ, however, in their venation but differ therefrom in the absence of scales from the wings. The larva of *Dixa* frequents shady, weedy pools or streams and might be mistaken for that of *Anopheles*. It is eucephalous with 12 trunk segments, the 4th and 5th each bearing a pair of ventral pseudopods armed with curved spinules: segments 5–10 in certain species carry a dorsal shield fringed by setæ. The pupa closely resembles that of the Culicidæ. For the British species vide Edwards (*Ent. Month. Mag.*, 1920).

FAM. CULICIDÆ (Gnats or mosquitoes).—VERY SLENDER FLIES, GENERALLY WITH AN ELONGATE PIERCING PROBOSCIS AND NO OCELLI: THE PALPI STIFF AND NOT PENDULOUS. LEGS LONG, ANTENNÆ DENSELY PLUMOSE IN THE MALES, PILOSE IN THE FEMALES. WINGS FRINGED WITH SCALES ALONG THE POSTERIOR MARGIN AND THE VEINS. LARVÆ AND PUPÆ AQUATIC AND VERY ACTIVE: THE FORMER METAPNEUSTIC, WITH AN ENLARGED THORACIC MASS.

The remarkable discoveries in their life-histories, and the part played by the adults as disease carriers, has given an enormous stimulus to the study of mosquitoes. More than 1,600 species have been described and at least 28 species occur in Britain. Culicidæ are almost world-wide in distribution, but the tropics are much richer in genera and species than northern latitudes. In arctic regions they are extremely abundant during the short summer, though few in species. In these parts they often occur far from the haunts of man and frequently in regions uninhabited by quadrupeds. In Lapland their numbers even exceed those of most tropical regions. For a full account of the biology of the family the student is referred to the standard treatise by Howard, Dyar, and Knab (1912). For the anatomy of mosquitoes vide Nuttall and Shipley (1901–03), and Christophers (1901). For the larval anatomy of *Anopheles* vide Imms (1907–08) and of *Culex* vide Raschke (1887). The mouthparts of a mosquito have already been described (p. 620): in the Chaoborinæ they are very short, concealed, and not adapted for piercing. Except in a few genera the whole body, legs and wings are in part, or entirely, clothed with scales.

The eggs are deposited on or near the surface of the water, and the number laid by a single individual varies from 40–100 (*Anopheles maculipennis*) up to 300 or more (*Culex pipiens*). They may occur singly, as in *Anopheles* or *Stegomyia*, or collectively to form a compact mass or egg-raft as in *Culex* (vide Miall, 1895) and other genera.

The eggs vary in shape in different genera: those of *Anopheles* are boat-shaped with a conspicuous float on either side: in *Culex* they are fusiform, in *Megarhinus* somewhat club-shaped, while those of *Stegomyia* are ovoid and surrounded by a series of small air chambers which aid in floating.

Mosquito larvæ have a well developed mobile head: the eyes vary according to the age of the larva and, as a rule, both the primitive larval eyes and the developing compound organs of the imago are present. A pair of dense tufts of long hair, or feeding brushes, are present over the mouth on either side of the head. By means of the movement of these brushes a current is set in motion which wafts microscopic food-particles towards the mouth. The thoracic segments are fused to form a single broad rounded region. Nine abdominal segments are present, and the anal somite is surrounded at its apex by four tracheal gills. These organs are small in surface feeders such as *Anopheles*, but larger in *Stegomyia* which is a bottom feeder. The respiratory system is metapneustic, and opens on the dorsal surface of the 8th segment. The spiracles are placed either on a quadrilateral area raised slightly above the preceding segment (Anophelinæ), or more usually at the apex of a respiratory siphon. The larvæ of *Chaoborus* (vide Akehurst, *Journ. Roy. Mic. Soc.* 1922) is a highly specialized type, being almost completely transparent and apneustic. It is provided with a pair of pigmented air-sacs in the thorax and a second pair in the 7th abdominal segment: these structures act as organs of flotation, respiration being cutaneous.

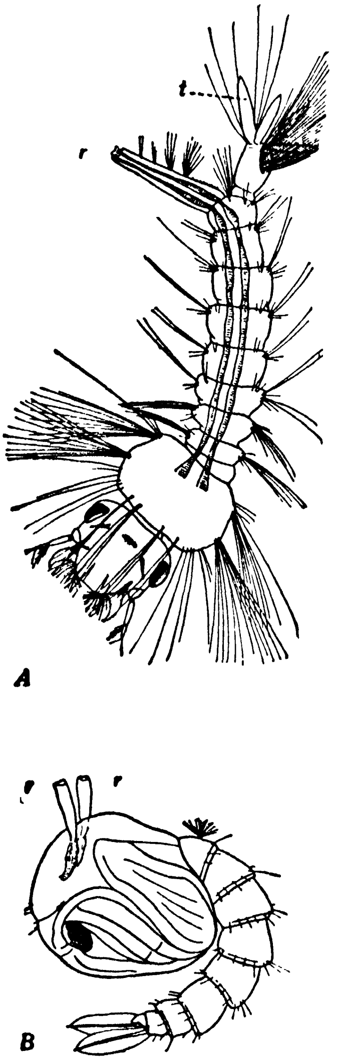

Fig. 591.—*Culex pipiens.*

A, larva; *B*, pupa; *r*, respiratory siphon; *t*, tracheal gills. From Folsom's "Entomology."

When at rest, and during feeding, the larvæ of Anophelines float horizontally just beneath the surface-film with the palmate hairs and spiracular area in contact with the latter. In the Culicines the larvæ bring the apex of the siphon in contact with the surface and hang head downwards, inclined at an angle with the surface film.

In their feeding habits, mosquito larvæ may be phytophagous or carnivorous. As a rule they feed upon minute algæ and other particles contained in the water. Certain forms, however, are carnivorous. These may be readily recognized either by the mouth-brushes being replaced by stout spines, which serve to seize the prey, or by the prehensile antennæ (Chaoborinæ). The organisms most frequently preyed upon are other mosquito larvæ.

As a rule, mosquito larvæ are only able to exist in small numbers in permanent waters on account of the presence of predaceous organisms, such as fish and insect larvæ Their habitat is extremely varied, thus *Anopheles lutzi* breeds in the cups of epiphytic and pitcher plants. Those of *A. rossi* frequent shallow rain-filled pools such as abound in India during the monsoon. *A. ludlowi* occurs in pools flooded by the sea at high tides: larvæ of *Tæniorhynchus* live at the roots of aquatic plants in swamps, inserting their modified siphons into the tissues, and thus deriving their supply of oxygen. *A. listoni* frequents sub-Himalayan hill streams; *A. chaudoyei* lives in the waters of Saharan oases containing 40 grms. of chlorides per litre and *A. stevensi* abounds in Bombay, living in the waters of wells and cisterns. The pupæ are very active, and respire by means of a pair of breathing trumpets communicating with the anterior spiracles. They float at the top of the water with their trumpets attached to the surface film.

When at rest Anophelines can usually be distinguished from other mosquitoes by the fact that they settle with the proboscis and the long axis of the body in one straight line, while in the Culicines the abdomen is usually parallel with, or inclined towards, the surface upon which the insect rests (Fig. 592). The length of the life-cycle of mosquitoes is primarily dependent upon temperature: thus, that of *S. fasciata* is normally 15–20 days, but may be as short as 11 days. The adult refuses to feed below 23° C. and is quite inactive at 20° C.

Economically mosquitoes are of the utmost significance owing to their functioning as the intermediary hosts of malaria, yellow fever, filariasis, dengue and other diseases. Increased knowledge of these insects, and the diseases transmitted by them, has rendered vast areas of tropical countries no longer a menace to the life of the European. The experimental researches of Ross, on the malaria *Plasmodium*, have conclusively proved that this parasite passes through two periods of multiplication during its life-cycle: the first is one of asexual reproduction (schizigony) and occurs in the blood of man. The second or sexual cycle (sporogony) takes place in the mosquito, and commences with the entry of blood containing suitable forms of the parasite into the stomach of the insect. After fertilization the xygote bores into the gut-wall where it becomes encysted. The cyst increases enormously in size, and eventually ruptures, liberating great numbers of sporozoites into the hæmocœlic cavity of the insect. Those sporozoites, which bore their way into the salivary glands, are then able to be transmitted to another human being through the punctures of the mosquito, and there continue their development.

When the female mosquito feeds the tip of the labium is first brought against the skin, and then the pointed mandibles and maxillæ are inserted. The labrum is also inserted into the puncture along with the hypopharynx. The labium is then doubled back in the form of a loop as the mouth-parts become more deeply inserted. According to Macgregor (*Trans. Roy. Soc. Trop. Med. and Hyg.* 24, 1931) two methods of feeding occur. In the method just described the ingested food is drawn continuously into the stomach. In the second method, termed "discontinuous feeding," the mouth-parts are not disengaged from the labium and the tip of the proboscis is merely dipped from time to time below the surface of the fluid to be imbibed. The ingested food then passes first to the œsophageal diverticula which act as food reservoirs. These organs also function as air separators in which "air locks," between discontinuous sections of fluid, are removed before such fluid passes into the stomach. Control is exercised over ingested foods to the extent that blood is allowed to pass to the stomach and sugary solutions into the diverticula. It appears that in *Stegomyia* the entry and digestion of blood in the stomach is a necessary condition for ovulation.

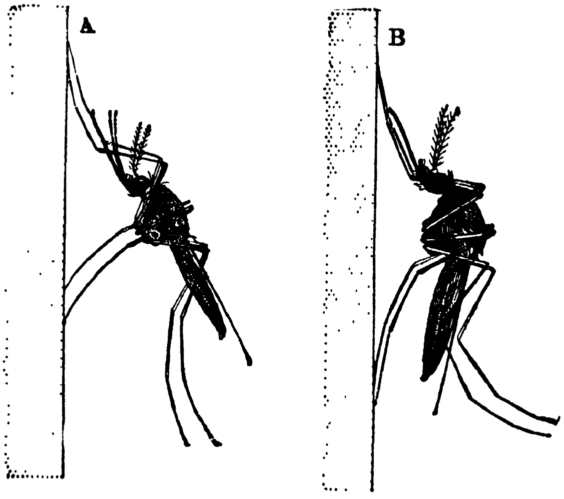

FIG. 592.—RESTING ATTITUDES OF *A*, *ANOPHELES* *B*, *CULEX*.

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A number of Anopheline mosquitoes are now known to be carriers of the plasmodia of one or more forms of malaria and, as the habits of these species greatly vary, a knowledge of their bionomics is of the highest importance from the standpoint of public health. Among the more important carriers are *Anopheles maculipennis* (Europe, parts of United States), *A. culicifacies* (India), *A. costalis* and *A. funestus* (Africa), *A. albimanus* (Central and S. America), *A. quadrimaculatus* (U.S.).

Stegomyia fasciata (*calopus*) [1] is one of the commonest mosquitoes of the tropics and subtropics of the world, and occurs largely along coasts and the courses of the larger rivers. In 1881 Finlay observed the incidence of this mosquito and yellow fever in Cuba, and succeeded in transmitting the disease through the agency of its punctures. In 1899 an American Commission sent to Cuba definitely proved that yellow fever is carried by *S. fasciata*. As the result of anti-*Stegomyia* measures in the Panama Canal zone, which was at one time a notorious region for this disease, yellow fever has become practically non-existent. The eggs of this mosquito are laid upon any accumulation of stagnant water however small, old tins, broken bottles, holes in trees often being utilized. The larva of this species may be recognized by its comparatively colourless appearance, and the short black respiratory siphon, ¼ the length of the abdomen. The adult is most easily identified by the lyre-shaped white mark on the thorax: it is essentially a domestic species rarely found away from towns and villages.

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[1] The most recent name for this species is *Aedes ægypti*.

Culex fatigans is an almost tropicopolitan mosquito of great economic significance. Along with other species it is a carrier of *Wuchereria bancrofti* which produces elephantiasis Both *C. fatigans* and *Stegomyia fasciata* are able to transmit the virus of dengue from one human being to another. *Anopheles maculipennis, Culex pipiens, Stegomyia fasciata,* etc., are intermediary hosts of *Filaria immitis* of the dog and several species of Culicidæ transmit the Plasmodium of avian malaria from one bird to another.

Various measures concerned with the control of mosquitoes have been introduced. Freedom from the attacks of these insects is largely obtained by living in mosquito proof dwellings or by utilizing mosquito curtains while sleeping. A variety of deterrent substances have been recommended for application to the exposed parts of the body: essential oils of various kinds have been more especially advised. The destruction of adult mosquitoes in dwellings may be carried out by the fumigation of rooms by means of cresyl: traps in the form of boxes, lined with dark blue cloth, which may be readily closed, have also been recommended. The removal of herbage from the neighbourhood of dwellings is a further measure. The elimination of all standing water, and the drainage of marshy lands, afford the principal means for reducing the larval breeding places. The screening of tanks and wells, etc., is also of importance. Application of larvicides such as kerosene, which will form a film on the surface of standing water, prevents the larvæ from coming to the surface to breathe, and provides a deterrent to egg-laying females. Tanks and irrigation canals in the tropics may be stored with certain fish (Cypriondontidæ, etc.) which are known to devour mosquito larvæ.

The literature on Culicidæ is very extensive and one of the best general works on the family is that of Howard, Dyar and Knab (1912) which deals with the species of North and Central America. The palæarctic species have been revised by Edwards (*Bull. Ent. Res.*, 1921) and those of North and South America have been revised by Knab (*Carnegie Inst., Publ.* No. 387, 1928). A useful handbook of the British mosquitoes has been written by Lang (1920).

FAM. CHIRONOMIDÆ (Midges).—DELICATE GNAT-LIKE FLIES: ANTENNÆ CONSPICUOUSLY PLUMOSE IN THE MALES, PILOSE IN THE FEMALE. HEAD SMALL, OFTEN CONCEALED BY THE THORAX: OCELLI ABSENT. MOUTH PARTS USUALLY POORLY DEVELOPED, SELDOM ADAPTED FOR PIERCING. ANTERIOR WING-VEINS MORE STRONGLY MARKED THAN POSTERIOR. LARVÆ APNEUSTIC: AQUATIC OR TERRESTRIAL.

These insects bear a general resemblance to Culicidæ but may be distinguished by the wings being unscaled. The adults occur in great numbers in the vicinity of lakes, ponds and streams: many appear on the wing just before sunset, and exhibit a characteristic gregarious habit of "dancing" in the air in swarms. During these evolutions the number of females present does not appear to be large and, when pairing is accomplished, the mated couple leave the swarm. Considerably over 1,000 species have been described: in Britain nearly 200 species are listed by Verrall, but many more await discovery. The antennæ are 6- to 15-jointed and, except in the Ceratopogininæ, the mouth-parts are poorly developed. In *Chironomus* no food is taken during adult life and the digestive canal is consequently shrunken and empty. In the Ceratopogininæ blood-sucking habits are frequent and, in such cases, a short piercing proboscis is present. Species of *Culicoides* (especially *C. pulicaris* L.) often cause a good deal of annoyance by means of their sharp punctures: several species of the sub-family have been observed to suck the inner contents of caterpillars and other insects.

The eggs of Chironomidæ are laid in a mass, enveloped by transparent mucilage secreted by the gluten gland of the female: these egg-masses or ribbons vary in shape and number, and arrangement of the eggs therein, in different species. The larvæ usually inhabit slow streams and ponds, or even puddles or water troughs. A few species can live at great depths, having been obtained from the bottom of Lake Geneva and Lake Superior. Several species occur in the sea, both in shore pools and at a depth of 15–20 fathoms: vast numbers frequent the salt lakes adjoining the Suez Canal. A typical kind of Chironomid larva, such as that of *C. dorsalis*, has a well-developed head and 12 trunk segments, with a pair of pseudopods on the prothorax and last abdominal segment: in other forms pseudopods are present on the prothorax only or, more rarely, are absent. Two pairs of elongate blood-gills may be present on the 11th segment, and two pairs of papilla-like anal gills are placed around the anus. In *C. dorsalis* the tracheal system is greatly reduced and limited to the thorax, where there are two pairs of closed spiracles. A number of species are red, owing to the presence of hæmoglobin dissolved in the blood-plasma, and are commonly known as "blood-worms." It was pointed out many years ago by Lankester that hæmoglobin occurs among invertebrates when increased facilities for oxidation are required, as by burrowing forms and those which lurk in the mud of stagnant pools. Surface-haunting Chironomid larvæ are generally green. The larvæ usually live in tubes either free, or attached to stones, etc., and composed of mud particles or of vegetable fragments, sticks, particles of green leaves, Confervæ, etc. The pupæ may be active (*Tanypus*), float at the surface of the water, or remain at the bottom of the water: in the latter case they rest in the old larval tube which is often provided with the addition of an operculum. The pupal respiratory organs either consist of a pair of much branched filaments, or of simple tubes: they are rarely absent.

The Ceratopogoninæ fall into two groups—those with aquatic, vermiform larvæ whose imagines are more or less bare-winged (*Culicoides, Bezzia*) and those with terrestrial larvæ found in sap, under bark or in decaying organic matter. The latter include *Forcipomyia* and *Dasyhelea* whose imagines have hairy wings. The distinctions, however, are not absolute as some larvæ of *Culicoides* are terrestrial and certain of those of *Forcipomyia* are aquatic. For the British species, see Edwards (1926). The best account of the larvæ is that of Saunders (1924–25).

The Clunioninæ include certain remarkable maritime genera whose larvæ live among algæ, and the adults are apterous. Among them are *Belgica* Jac. from Patagonia, *Halirytus* Eaton, Kerguelen I, and the European *Clunio* Hal, the males of which are winged. For an account of marine Chironomids see Edwards (1926A).

Parthenogenesis is known to occur in a few Chironomids and results in the production of females only. The first observations were made by Grimm on *Tanytarsus* in 1870 and have been confirmed by Zavrel. Both the pupæ and newly-emerged imagines are parthenogenetic. *Corynoneura celeripes* Winn. and *Chironomus clavaticornis* Kieff. also lay parthenogenetic eggs (Edwards, 1919). Pædogenesis has been ascertained to occur in the larva of *Tanytarsus dissimilis* by Johannsen in America (*Science*, 1910, p. 768). For the classification of the family vide Kieffer (1919), and a good deal of general information will be found in the works of Johannsen (1905), Malloch (1915, 1915A), Miall and Hammond (1900) and Goetghebuer (Faune de France).

FAM. CECIDOMYIDÆ (Gall Midges).—MINUTE DELICATE FLIES WITH LONG MONILIFORM ANTENNÆ ADORNED WITH CONSPICUOUS WHORLS OF HAIR; OCELLI PRESENT OR ABSENT. WINGS WITH FEW LONGITUDINAL VEINS, FOR THE MOST PART UNBRANCHED, AND WITH NO OBVIOUS CROSS-VEINS. COXÆ NOT ELONGATE, TIBIÆ DEVOID OF SPURS. LARVÆ PERIPNEUSTIC WITH A REDUCED HEAD AND USUALLY A STERNAL SPATULA.

The Cecidomyidæ include a large number of fragile and often very minute insects. The antennal characters, and the greatly simplified venation, enable these midges to be easily recognized. Among the best known species is the Hessian fly (*Mayetiola destructor*) whose larvæ are often destructive to wheat (vide Enoch, 1891); from Europe it has been introduced into N. America and New Zealand. The Pear Midge (*Contarinia pirivora*) is one of the most serious pests of that fruit in Europe; its larvæ feed gregariously in the young fruitlets, which become deformed and subsequently decay.

The best general monograph on the family is that of Kieffer (1900) while the plant galls are described and catalogued by Houard. A good deal of information is also given in the numerous reports of Felt, and most of the British galls are dealt with in the works of Connold and Swanton; for the Cecidomyids affecting cereals vide Marchal (1897).

Larval Cecidomyidæ exhibit great diversity of habits and may be classified as follows:

I. Zoophagous species of which very few are true parasites: Keiffer instances *Endaphis pervidus* Kief. which parasites *Drepanosiphon platanoides* Schr. A considerable number are predaceous, preying mainly upon Homoptera, but others attack Acari; a few (species of *Lestodiplosis*) attack dipterous larvæ and pupæ, including those of other Cecidomyidæ.

II. Saprophagous species. Kieffer records species which live among the excrement of Tipulids and lepidopterous larvæ, and a few are found among decaying vegetable matter.

III. Phytophagous species which may be divided into *a.*—Those which live on or within various parts of plants without producing any gall formation. A number of species live on the spikelets of Graminæ, others in the flowers of Compositæ, in fruit, or among Fungi. *b.*—Gallicolous forms: a few live in galls formed by Coleoptera, Trypaneidæ, and other Cecidomyidæ. *c.*—Cecidogenous or true gall-making species. The vast majority of the family come under this category and all parts of the plant may be affected. Felt (1911) computed that 438 species, included in 44 genera, of American Cecidomyidæ affected 177 plant genera comprised in 66 families. Of these 146 species formed bud-galls, 44 fruit-galls, 218 leaf-galls, 130 stem-galls, and 4 formed root-galls. The Compositæ, Salicaceæ and Gramineæ are the most frequently selected both in America and Europe. One of the most generalized of true gall-makers is *Rhabdophaga* which is partial to *Salix*, producing simple deformities such as bud and subcuticular galls. *Dasyneura* also forms comparatively simple leaf- and bud-galls on various plants.

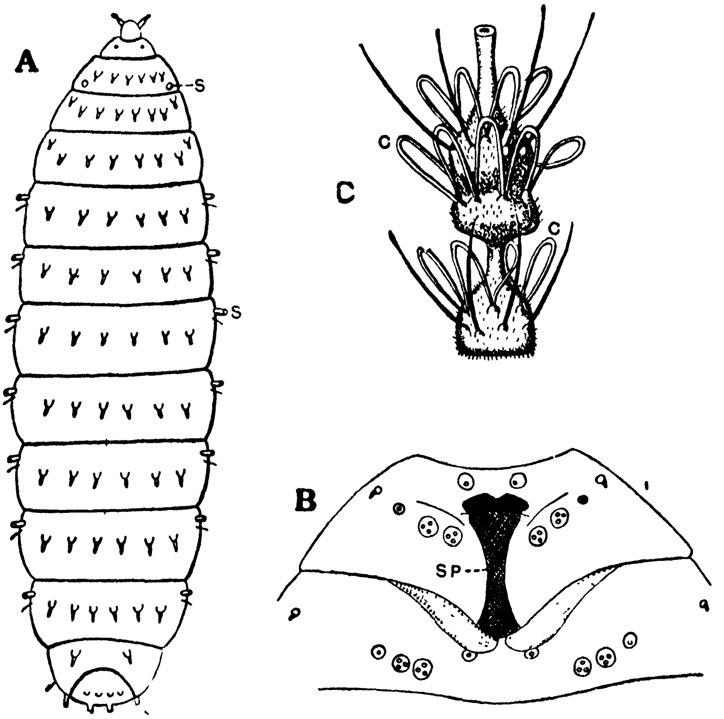

FIG. 593.—A, LARVA OF *CONTARINIA PIRIVORA*, DORSAL VIEW; *s*, spiracles. B, VENTRAL ASPECT OF 1ST THORACIC SEGMENT (1) SHOWING STERNAL SPATULA SP. C, ANTENNAL JOINT OF *XYLODIPLOSIS PRÆCOX* MALE SHOWING CIRCUMFILI *c*.

Adapted from Kieffer, *Ann. Soc. Ent. Fr.* 1900.

The larval structure is dealt with at length by Kieffer, and the larvæ are usually rather short and somewhat narrowed at both extremities. They vary in colour, being frequently white, yellow, orange or bright red, and occasionally brown. The head is very small and incompletely differentiated; pigment spots are present but there are no eyes. Thirteen trunk segments are evident, the first being intercalated between the head and prothorax. There are nine pairs of spiracles situated on the prothorax and first 8 abdominal segments. According to Kieffer the larva of *Rhinomyia perplexa* is exceptional in possessing 10 pairs, the additional pair being situated on the anal segment. The most characteristic structure associated with Cecidomyid larvæ is the sternal spatula or so-called " breast bone " (Fig. 593), which is situated mid-ventrally on the thorax. It is an elongate, chitinized sclerite either toothed, pointed, or bi-lobed anteriorly: in some genera it is wanting. The function of this organ has been variously interpreted as an organ of perforation used for abrading plant tissues, as a locomotory organ, or for changing the position of the larva in its cocoon or case. Many larvæ possess the power of leaping (*Contarinia*, etc.) and, according to Giard, in performing this act the anal crochets lock into the extremity of the spatula. The larva is thus curved into a loop, perpendicular to the surface upon which it is resting. By means of a sudden release of the tension it may be projected a distance of several centimetres.

Two methods of pupation occur in Cecidomyidæ. In the usual method the pupa is enclosed in a cocoon which may be either single or double: in *Mavetiola* and *Chor-*

tomyia the outer layer has the appearance of a puparium and is formed by the persistent larval skin.

The adults usually bear *circumfili* on the antennæ: they are best developed in the males and are curious looped filaments or tortuous threads. In *Contarinia* and its allies each loop is fused basally with its fellows, thus producing an apparent whorl around each segment (Fig. 593 C). Their function is obscure, but it is presumably sensory. For the occurrence of pædogenesis in this family, see p. 164.

FAM. MYCETOPHILIDÆ (Fungus Gnats).—SMALL FLIES PROVIDED WITH OCELLI, ANTENNÆ LONG, USUALLY LACKING WHORLS OF HAIR IN THE MALE; COXÆ ELONGATE, TIBIÆ SPURRED. LARVÆ SMOOTH AND VERMIFORM WITH A SMALL DARK HEAD, EIGHT PAIRS OF SPIRACLES, AND LIVING GREGARIOUSLY IN FUNGI OR DECAYING VEGETABLE MATTER.

The fungus gnats are delicate flies of a small or medium size, often bearing a resemblance to gnats or midges, and exceedingly numerous in individuals and species. Upwards of 2,000 species are known, and the geographical range of the family is very wide. In coloration fungus gnats are seldom striking—blacks, browns and yellowish hues predominating. The body is elongate and compressed, with the thorax more or less arched, and sometimes markedly so. The antennæ (Fig. 578) are almost always long and filiform, and composed of 12–17 joints, 16 being a common number. The tibiæ are slender and armed with apical spurs, and the tarsal claws are toothed or pectinate. Sexual dimorphism occurs in a few species of the *Sciarinæ*. In *Sciara semialata* Edw. for example, the male possesses greatly reduced wings while the female is normal. In *Epidapus scabiei* Hop. the female is destitute of both halteres and wings, while the male exists in two forms—one with reduced and the other with normal wings.

The larvæ of a number of species have been described and the valuable paper by Osten Sacken (1862) should be consulted together with more recent work by Malloch (1917) and Keilin (1919A). They are soft and whitish, with a small black or brown strongly chitinized head, and 12 body segments. They are elongate and vermiform in shape, and generally sufficiently transparent to reveal much of their inner anatomy. The cuticle is smooth and devoid of hairs or setæ; on the ventral surface there are often transverse swellings which, in many cases, are furnished with minute spines aiding in locomotion. The antennæ are always very short and frequently almost absent; they are better developed in *Bolitophila* than in most other genera. Situated below the antennæ an oval pellucid spot is often present (*Bolitophila, Mycetophila, Leia, Epidapus,* etc.) which is probably of the nature of an ocellus. The respiratory system is peripneustic with 8 pairs of spiracles. The latter are found on the prothoracic and first 7 abdominal segments, the prothoracic pair being the largest. Exceptional genera include *Ditomyia* and *Symmerus* with 9 pairs of spiracles (Keilin, 1918A); *Platyura* is stated to be devoid of spiracles and provided with protrusible anal gills and *Polylepta*, according to Schmitz, is propneustic.

The imagines are found in a variety of situations, most commonly in damp or dark places, where there is fungoid growth, or decaying vegetation. Cellars, sheds, manure heaps and damp secluded parts of woods furnish many species. One of the characteristic features of these flies is their power of leaping, the hind-legs being adapted for the purpose; many species simulate death when disturbed. The popular name of fungus gnat is derived from the fact that the larvæ feed upon fungi more often than any other substance. A number of species however are found in rotting wood and other decaying organic matter, including leaf-mould and manure. The larvæ are markedly gregarious, and many species construct a loose slimy web on their pabulum. Those of *Leia, Sciophila* and *Ceroplatus* are very active, gliding with great facility, either backwards or forwards, enveloped by the tube-like sheath of threads composing the web. Others, such as *Exechia*, burrow within their substratum lining the tunnels with a slimy secretion. The larva of *Mycetophila ancyliformans* Holmg. is exceptional in its mode of life, having been found living singly and exposed on the leaves of a bamboo in S. America. It is protected by a remarkable covering of excrementous particles which may be readily mistaken for an *Ancylus* shell, so close is the resemblance.

Larvæ of the Sciarinæ have been found in decaying apples, pears, turnips, potatoes, etc., and sometimes attack seedlings. In certain species of *Sciara* they exhibit the curious habit of travelling in vast numbers, so closely together as to almost constitute a single mass. This phenomenon is not infrequent at certain seasons in woods in Germany, Sweden, Russia and also in N. America. The migratory columns are elongate in form, and have been termed " snake worms " in the United States, on account of their snake-like movements and appearance, which are said to resemble a thin gray reptile. They progress as a single mass with the larvæ several deep over each other, and the movement is stated to be at the rate of about an inch a minute. In Europe they have been termed the "army worm," but in America this expression is more properly applied to certain Noctuid caterpillars. Lintner mentions the stream of larvæ as often being 12–15 ft. long, 2–3 inches broad, and perhaps ½ inch in thickness. In the United States one species has been reared and identified as *Sciara fraterna*; the common European "army worm" is *Sciara militaris*. No satisfactory explanation has yet been advanced to account for the assemblage of these hordes of footless larvæ. Berthold regards the phenomenon as a collection of larvæ for the purpose of mutual protection prior to pupation. Beling believes that they are marching for the purpose of moving to a fresh feeding ground, but as they are usually fully fed when the phenomenon occurs this explanation is open to doubt.

Several species exhibit luminosity, which appears to have been first observed in the larvæ and pupæ of *Ceroplatus sessiodes* by Wahlberg in 1838. A particularly brilliant light was observed by Hudson in a New Zealand species (*Bolitophila luminosa*), who remarks that the light emitted from a single larva kept in a caterpillar cage may be seen streaming out of the ventilators at a distance of several feet. Wheeler and Williams (1915) describe it as being emitted from the distal portion of the malpighian tubes. The pupa and female imago are also strongly luminous but, according to Norris (*Ent. Month. Mag.*, 1894), the male does not exhibit this property.

Some Mycetophilids spin true cocoons for pupation while others construct a fragile case of earthy material: the pupa in *Leia* is simply suspended by means of loose threads. In *Epicrypta* the larval skin is adapted to form a shell in which to pupate but the pupa itself is free. The eggs are laid singly or in small groups, occasionally in strings, on whatever substance serves as food for the larvæ. Many species pass through several generations in the course of a year, and as a general rule larval and pupal life is of short duration although certain species hibernate as pupæ. According to Johannsen the time occupied from the egg to the adult may not exceed two weeks in midsummer. Edible mushrooms are frequently attacked by larvæ of *Sciara*, *Exechia* and *Mycetophila*. They completely riddle the plants and may ruin a whole mushroom bed. Not infrequently they are introduced into the mushroom cellars through the agency of the manure used in the beds. According to Hopkins there are forms of potato scab and rot which are not due to fungoid disease, but are the direct result of the attacks of species of *Sciara* and *Epidapus*. *Sciara tritici* Coq. damages roots and stems of young wheat plants, and Johannsen remarks that there is no lack of evidence that Sciarinæ damage the roots of cucumbers, grass and potted plants.

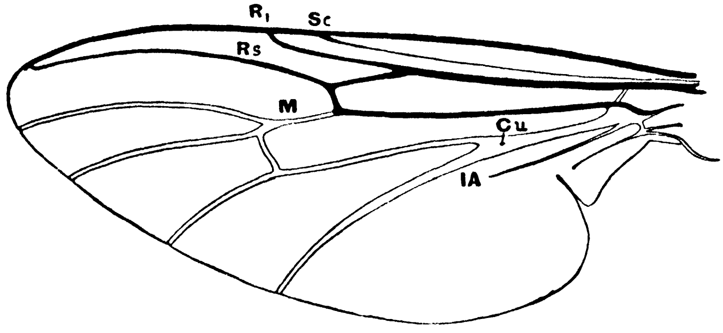

FIG. 594.—*BIBIO MARCI*, VENATION.

The most important recent works on the family are the monographs of Johannsen (1909) and the account in Lindner's textbook. Information concerning British Mycetophilids is given by Edwards (1913, 1925).

FAM. BIBIONIDÆ.—ANTENNÆ 8 TO 16-JOINTED, USUALLY SHORTER THAN THE THORAX, THE JOINTS BEAD-LIKE AND CLOSELY APPOSED (Fig. 578). WINGS LARGE, ANTERIOR VEINS MORE STRONGLY MARKED THAN POSTERIOR (Fig. 594). EYES IN MALES HOLOPTIC OR APPROXIMATED, OCELLI PRESENT. LARVÆ TERRESTRIAL, PERIPNEUSTIC.

The Bibionidæ are robust flies, often pubescent with shorter legs and wings than most other Nematocera. In the males the eyes often occupy nearly the whole of the head and the upper facets are much larger than the lower, the two series being sharply differentiated. Certain species exhibit colour dimorphism, the females often being reddish-brown while the males are entirely black.

The species of the sub-family Bibionidæ frequent meadows, grassy hillsides or decaying vegetation and often appear in great numbers. Their larvæ feed at the roots of grasses, cereals, hops and in leaf mould. Those of *Bibio* (vide Morris, 1921–22) are often gregarious and, structurally, they are the most primitive of all dipterous larvæ. They are 12-segmented with a large exserted head, well developed mouthparts and are devoid of pseudopods (Fig. 595). Each segment is provided with a band of short fleshy processes, the latter attaining their greatest length on the 11th and 12th segments: the first segment is transversely divided and carries two bands of these processes. Open spiracles are present on each segment except the 2nd and 11th, the hindmost pair being considerably larger than its fellows. Pupation occurs in an earthen cell below ground.

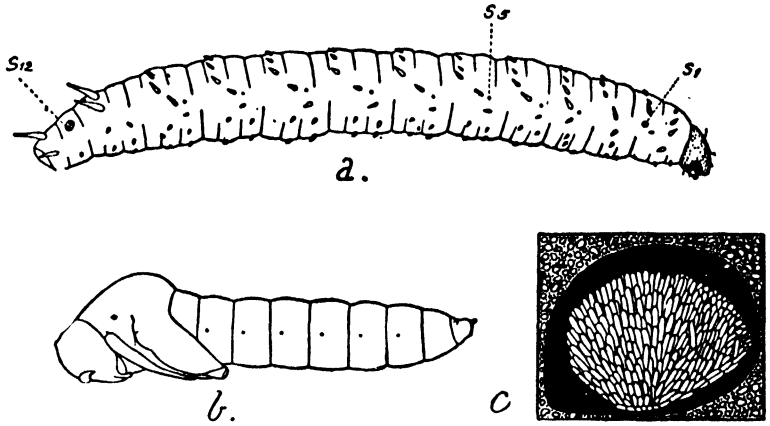

FIG. 595.—*BIBIO MARCI.*

a, larva: s_1, s_8, s_{12}, spiracles of their respective segments; *b*, pupa; *c*, egg-mass in subterranean chamber. *After* Morris, *Bull. Entom. Res. 1921.*

The Scatopsinæ are regarded by some authorities as constituting a separate family. Their larvæ live in decaying organic matter and pupation takes place in the persistent larval skin. In *Scatopse* (Morris, 1918) the larva is provided with longitudinal and transverse bands of hairs: nine pairs of spiracles are present on the 1st segment and on the 4th to 11th segments respectively, the hindmost pair being carried on stout chitinous pedicels. The 11th segment bears two posteriorly directed processes fringed with long hairs. For the British Bibionidæ, see Edwards (1925).

FAM. SIMULIIDÆ—SMALL STOUTLY BUILT FLIES WITH SHORT LEGS AND ELONGATE MANDIBLES. WINGS BROAD, ANTERIOR VEINS THICKENED, THE OTHERS FAINT. ANTENNÆ 11-JOINTED, SCARCELY LONGER THAN THE HEAD: OCELLI WANTING, THE MALES HOLOPTIC. LARVÆ IN RUNNING WATER ATTACHED TO ROCKS BY THE ANAL EXTREMITY, SPIRACLES CLOSED.

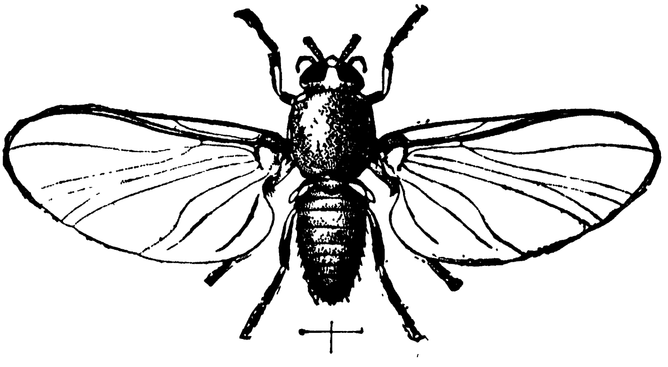

FIG. 596.—*SIMULIUM VENUSTUM* Say (= *REPTANS* L.), FEMALE. × 12. N. AMERICA.

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A small family of world-wide distribution and including the familiar "buffalo gnats" of America (Fig. 596). In the males the eyes have the upper facets markedly larger than the lower, and the 1st tarsal joint is usually much dilated. Both sexes possess elongated piercing mandibles which are broader in the female than in the male. The females of certain species are active blood-suckers and in some countries are veritable scourges. *S. indicum*, the "potu" fly, is a troublesome pest in parts of the Himalayas, and *S. columbaczense* Schönb. is at times a great scourge of man and domestic animals, particularly in regions bordering on the Danube. It often appears in enormous swarms and the flies attack the orifices of the body entering the ears, nostrils, margins of the eyes, etc., in great numbers, and their punctures produce an inflammatory fever often resulting in death. Certain other species are pests in many parts of N. America: *S. meridionale* Riley causes the death of numerous turkeys and chickens in Virginia, and *S. pecuarum* Riley is the common American buffalo gnat. In a few instances species of this genus have been observed to suck the blood of other insects. Sambon has advanced the theory that the disease in Italy known as pellagra is transmitted by *Simulium*. Outbreaks of this complaint are stated to be confined to those districts infested by the fly and to those periods when the insect is on the wing.

Adult Simuliidæ occur in the neighbourhood of streams and rivers; the eggs are laid either on herbage or stones, above or beneath the surface of the water. Britten (*Ent. Month. Mag.*, 1915) has observed the female of *S. maculatum* Mg. submerged to a depth of 1 foot during oviposition: the eggs are laid on vegetation and are coated with a gelatinous secretion.

The larvæ are invariably aquatic and require swiftly flowing water for their environment, and for this reason they are often found congregated in the vicinity of rapids and waterfalls, etc. Information concerning the metamorphoses of the family is given by Johannsen (1903–05), Meinert (1886), Puri (1925) and Jobbins-Pomeroy (*U.S. Agric. Dept. Bull.* 329). In the larvæ the head is complete and is characterized by the large maxillæ and the prominent mouth brushes. On the ventral aspect of the thoracic region there is a foot-like protuberance provided with hooklets: it functions as a kind of sucker and is formed by the fusion of a pair of pseudopods. On the anal segment there is a second sucker, armed with concentric series of stout hooklets and, associated with the anus, is a group of rectal gills which vary in number in different species. Nine pairs of minute spiracles are present from the mesothorax to the 7th abdominal segment; but respiration is performed by means of the rectal gills, which contain blood and are supplied with tracheoles (Taylor, 1902). The larvæ fix themselves to their substratum by means of the anal sucker and, as a means of locomotion, they loop the body after the manner of Geometrid caterpillars, bringing the anal extremity forwards beside the anterior sucker. Before pupation the larva forms a pocket-like cocoon open above; the pupal respiratory organs are composed of long tube-like filaments, which protrude from the cocoon and obtain oxygen from the moving water. For the British species of *Simulium* and their larvæ reference should be made to papers by Edwards (1915, 1920).

FAM. BLEPHAROCERIDÆ.—ELONGATE FLIES WITH LONG LEGS: EYES IN BOTH SEXES OFTEN HOLOPTIC, AND USUALLY BISECTED INTO AREAS OF DIFFERENT SIZED OMMATIDIA: OCELLI PRESENT. THORAX WITH TRANSVERSE SUTURE: WINGS WITH A COMPLEX NETWORK OR PERMANENT FOLDS. MOUTH-PARTS IN FEMALE ADAPTED FOR LACERATING. LARVÆ AQUATIC, ONISCIFORM, WITH VENTRAL SUCKERS.

A small family of very wide but discontinuous geographical range. It is confined to hilly or mountainous districts and is unrepresented in the British Isles. The adults frequent the borders of streams; they are weak fliers, and are less often met with than the larvæ. The females are predaceous, preying upon small Diptera, and the males probably feed upon nectar. The wings possess a fine network, or "secondary venation," of creases or folds in the membrane, which have not been obliterated after emergence from the pupa. The larvæ inhabit swiftly running hill streams where they fix themselves by means of their ventral suckers to rocks and stones, usually in places where the current is swiftest. The head, thorax and first two abdominal segments are fused together, and the remaining segments are deeply incised laterally. A longitudinal row of median ventral suckers, usually six in number, is their most characteristic feature: to the outside of each sucker is a group of digitate processes which are regarded by Kellogg as being tracheal gills. The tracheal system is peripneustic; the spiracles are minute and situated ventrally, but in all probability are closed. The pupæ are broad, and flattened beneath, adhering tenaciously to rocks, etc.: the respiratory horns are lamellate, and the legs extend almost to the apex of the abdomen. For a bibliography of the family together with a table of the larvæ vide Bezzi (1912); Kellogg's monograph (1907) and the important paper on the larvæ of Indian species by Tonnoir (1930) should be consulted.

FAM. DEUTEROPHLEBIIDÆ.—ANTENNÆ FILIFORM, VERY ELONGATE. WINGS WITH A NETWORK OF CREASES: OCELLI, MOUTH-PARTS AND TRUE VENATION ABSENT.

This small family consists of a single genus, *Deuterophlebia*, which is perhaps allied to the Blepharoceridæ and occurs in N. America and the mountains of Kashmir (vide Edwards, *Ann. Mag. Nat. Hist.* IX. 1922). Pulikovsky (*Trans. Ent. Soc. Lond.* 1924) has described the larva and pupa from streams in the Altai Mountains. The larva is provided with seven pairs of large segmental outgrowths bearing suckers, and it respires by means of anal blood-gills.

FAM. THAUMALEIDÆ (Orphnephilidæ).—ANTENNÆ OF TWO APPARENT JOINTS TERMINATED BY A 10- OR 11-JOINTED STYLE-LIKE APPENDAGE: PALPI LONGER THAN ANTENNÆ: EYES HOLOPTIC IN BOTH SEXES. LARVÆ AQUATIC, AMPHIPNEUSTIC, CHIRONOMID-LIKE.

A small family readily distinguishable from all other Nematocera by the structure of the antennæ. The adults are small sluggish insects and in Britain ***Thaumaleia testacea*** may be swept from grass and other herbage bordering hill-streams. The larva of this species has been described by Saunders (*Ann. Mag. Nat. Hist.* 1923), and in general appearance it resembles that of a Chironomid. Prothoracic and anal pseudopods are present, together with paired dorsal and blood gills, and spiracles are evident on the first and penultimate segments. The pupa is almost entirely covered with small warts which even extend on to the short respiratory horns. Its anal segment is provided with a pair of slender upwardly directed processes and two elongate setæ. For a revision of the family, see Edwards (*Zool. Anz.* 1929).

FAM. RHYPHIDÆ.—DISCAL CELL PRESENT: EYES IN MALE OFTEN HOLOPTIC, OCELLI EVIDENT. ANTENNÆ 16-JOINTED, ABOUT AS LONG AS THORAX. LARVÆ AMPHIPNEUSTIC, SAPROPHAGOUS.

A small family of gnat-like flies represented in all zoogeographical regions. In the presence of a discal cell *Rhyphus* (Fig. 34) differs from other Nematocera excepting the Tipulidæ, but is separable from the latter on account of the absence of the V-shaped mesonotal suture and the presence of ocelli. The whitish larva of this genus is well known (Perris, 1870; Malloch, 1917) and lives in decaying vegetable matter and manure. It is about 10 mm. long, elongate-cylindrical, and devoid of pseudopods. The thoracic segments are longer than broad, and those of the abdomen are separated by intercalary rings, giving the appearance of an increased number of segments. Spiracles are present on the prothoracic and last abdominal segments. The larva of *Mycetobia* [1] resembles that of *Rhyphus* (vide Keilin, 1919) and occurs in sap and in fungi found about decaying parts of trees. In *Trichocera* the larvæ live among fungi and decaying vegetation (Keilin, 1912). *Mycetobia* was placed for many years in the Mycetophilidæ until its affinities were reinvestigated by Edwards (1916) and Keilin.

Sub-order II. **Brachycera**

The Brachycera include fourteen families whose antennal characters are so varied, that the student will probably recognize many of its members more readily by means of the venation and the short porrect palpi. This applies particularly in the case of *Xylophagus*, *Rhachicerus* and *Cœnomyia* where the 3rd antennal joint is annulated to such an extent as to resemble the flagellum of some Nematocera and, furthermore, the style is wanting. It is also noteworthy that the discal cell is absent in the Dolichopodidæ and certain Empidæ. For a discussion of the affinities of the Brachycera and their larvæ the student is referred to the introductory pages of Verrall's work (1909). With the exception of the Stratiomyidæ, the head in brachycerous larvæ is usually retractile within the thorax. The tracheal system is typically amphipneustic, and rarely peripneustic or metapneustic. If we except Stratiomyidæ, the pupa is free and not enclosed in the larval skin: very rarely a cocoon is present (Dolichopodidæ and *Drapetis*). The pupæ may be recognized by their thorny appearance, spines being present on the antennal sheaths and other regions of the head and thorax. The abdominal segments are also usually provided with girdles of spines and the terminal somite is armed with pointed processes. The prothoracic respiratory organs are usually sessile.

Table of the Families of Brachycera:

1 (12).—Empodium pad-like nearly or quite as large as the two pulvilli.
2 (11).—Wing veins never running parallel with hind margin of the wing.
3 (8).—Third antennal joint annulated.
4 (5).—Vein C not entirely surrounding the wing. STRATIOMYIDÆ (p. 652)
5 (4).—Vein C entirely surrounding the wing.

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[1] The imago of *Mycetobia* is more closely related to the Mycetophilidæ than the Rhyphidæ and the discal cell is absent.

6 (7).—Squamæ large. TABANIDÆ (p. 654)
7 (6).—Squamæ vestigial. PANTOPHTHALMIDÆ (p. 654)
8 (3).—Third antennal joint not annulated, or, if annulated, an elongate flagellum present.
9 (10).—Squamæ extremely large: globular flies with small head. CYRTIDÆ (p. 656)
10 (9).—Squamæ vestigial: not such flies. LEPTIDÆ (p. 653)
11 (2).—A number of veins running parallel with the hind margin of the wing. NEMESTRINIDÆ (p. 656)
12 (1).—Empodium absent or represented by a bristle.
13 (16).—Flies clothed with dense furry pile.
14 (15).—M_3,M_4 separate except at apices: proboscis short. THEREVIDÆ (p. 658)
15 (14).—M_3,M_4 fused: proboscis usually elongate. BOMBYLIIDÆ (p. 659)
16 (13).—Flies not clothed with dense furry pile.
17 (20).—Flies devoid of bristles except in some cases on the legs.
18 (19).—Antennæ not terminating in a jointed club: R_1 short. SCENOPINIDÆ (p. 657)
19 (18).—Antennæ terminating in a club: R_1 long. MYDAIDÆ (p. 657)
20 (17).—Bristly flies.
21 (24).—Cubital cell long and pointed.
22 (23).—M_1 terminating before the apex of the wing: proboscis not adapted for piercing. APIOCERIDÆ (p. 657)
23 (22).—M_1 terminating a good way beyond the apex of the wing: proboscis horny and adapted for piercing. ASILIDÆ (p. 658)
24 (21).—Cubital cell usually short.
25 (26).—Proboscis horny, often long: very rarely metallic green flies. EMPIDÆ (p. 660)
26 (25).—Proboscis short and fleshy: metallic green or bluish flies. DOLICHOPODIDÆ (p. 661)

FAM. STRATIOMYIDÆ.—BRISTLELESS FLIES WITH THE 3RD ANTENNAL JOINT ANNULATED, SQUAMÆ VERY SMALL, TIBIÆ ALMOST ALWAYS WITHOUT SPURS; AND THE SCUTELLUM CONSPICUOUSLY DEVELOPED, OFTEN WITH SPINES OR PROJECTIONS. WING VEINS CROWDED NEAR COSTA AND MORE STRONGLY MARKED THAN THOSE BEHIND: C NOT ENCOMPASSING THE WING. PULVILLI AND AROLIUM PAD-LIKE.

The Stratiomyidæ (Fig. 598) are small to rather large flies, more or less flattened and usually with white, yellow, or green markings: in the Sarginæ, however, the prevailing colour is metallic green. Considerably over 1,000 species are known and of these about 50 are British. They are not strong fliers and occur on umbelliferous and other flowers and herbage, especially in damp situations. The Xylomyinæ are the most aberrant members both as regards their venation and the presence of tibial spurs: they are annectant between this family and the Leptidæ. Many authors have united *Xylomyia* with the Leptid genus *Xylophagus* to constitute a separate family—the Xylophagidæ, but we follow Osten-Sacken and Verrall in retaining the latter group in the Leptidæ.

The metamorphoses of a considerable number of Stratiomyidæ are known: the eggs are laid on plants near the edge of water, or even on the surface of water, also in dung or in the soil. The larvæ are carnivorous or saprophagous, and either terrestrial or aquatic, the terrestrial larvæ being large scavengers: those of the Xylomyinæ occur in rotting wood. Stratiomyid larvæ exhibit considerable diversity of form: all have a peculiar thick leathery skin impregnated with calcareous matter. The head is small and exserted, and there are 11 trunk segments, none of which bear pseudopods (Fig. 597). Although often described as being peripneustic, it is doubtful whether they are functionally so: they appear to be physiologically metapneustic or in some cases amphipneustic. The lateral spiracles, with the exception of the prothoracic pair, are minute and difficult to detect. In *Stratiomyia* 9 pairs are present; they are situated on the 1st and 3rd thoracic segments, and on each of the first 7 abdominal segments. Although stated by Brauer to be peripneustic, Miall remarks that the lateral spiracles are closed. The terminal or posterior spiracles are always open and are situated in a horizontal fissure, fringed with hairs in the aquatic forms. The larvæ of *Stratiomyia* and *Odontomyia* are greatly elongate and taper towards the anal extremity. In the former genus the last segment is much drawn out and tubular: these larvæ live in water or mud, and hang from the surface film by means of the tail coronet of feathery hairs which is spread out in an asteriform manner. When the larva descends, the hairs are drawn inwards and enclose a large air bubble: as the latter becomes used up the larva returns to the surface. The larva of *Xylomyia* resembles that of *Sargus*, being broad with parallel sides, and the usual leathery skin is impregnated with calcareous matter. It is regarded as being amphipneustic with prothoracic and terminal spiracles: according to Lundbeck nonfunctional lateral abdominal spiracles are also present. Stratiomyid pupæ differ from other Brachycera in being enclosed within the larval skin. Tables of the larval characters for each sub-family are given by Verrall (1909): further information will be found in the works of Lundbeck (1907) and Irwin-Smith (1920–23).

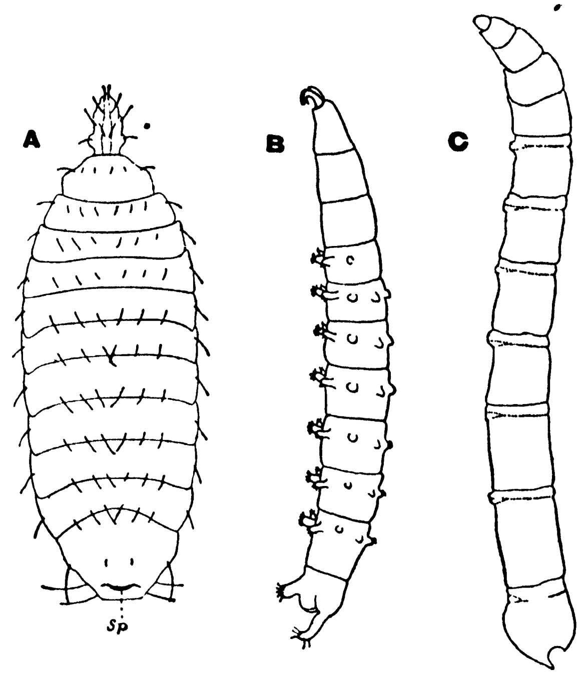

FIG. 597.—LARVÆ OF BRACHYCERA. *A*, *Microchrysa*; *Sp*, spiracles. *B*, *Tabanus*. *C*, *Leptis*.
A and *C after* Cameron, *Journ. Econ. Biol.* 8; *B after* King.

FAM. LEPTIDÆ.—BRISTLELESS FLIES; WITH THE 3RD ANTENNAL JOINT USUALLY NON-ANNULATED WITH A TERMINAL STYLE (Fig. 578). SOME OR ALL THE TIBIÆ SPURRED, SQUAMÆ PRACTICALLY ABSENT. WING VEINS WELL DEFINED, NOT CONTRACTED ANTERIORLY. PULVILLI AND AROLIUM PAD-LIKE.

The Leptidæ include rather elongate flies of sombre coloration, usually thinly pilose or almost bare (Fig. 599). Over 300 species have been described, of which about 19 are British. Normally they are predaceous upon other insects, but it is recorded that the female of *Symphoromyia* in America and *Spaniopsis* in Tasmania are bloodsuckers; the same habit has been stated to occur in *Leptis*, but further observations on the latter genus are needed. The Xylophaginæ and Cœnomyinæ are aberrant groups with the 3rd antennal joint annulated; their position has long been under discussion, and both have been elevated to family rank by several dipterists.

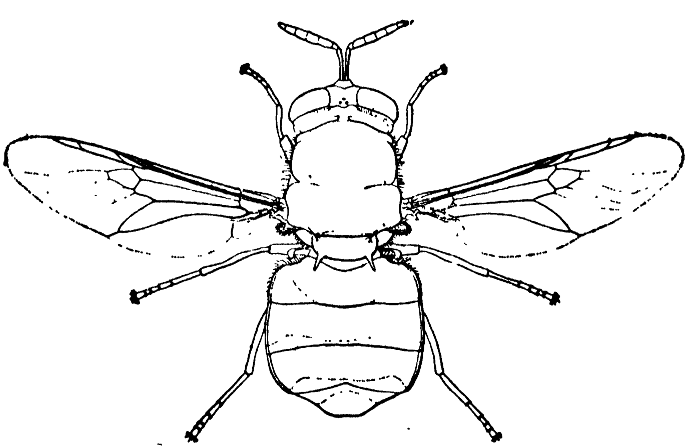

FIG. 598.—*STRATIOMYIA POTAMIDA*, FEMALE. × 4. BRITAIN.
After Verrall.

The metamorphoses of many Leptidæ are known (Beling, 1875, 1882: Greene, 1926); the larvæ (Fig. 597) are cylindrical, with a small exserted head succeeded by

11 trunk segments, which may or may not bear pseudopods. The abdominal segments often possess transverse denticulate, ventral swellings which aid in locomotion. The last segment is modified and marked by longitudinal folds or grooves, or provided with hairy processes. Leptid larvæ are carnivorous, preying upon other insects or their larvæ: according to Marchal the larva of *L. tringaria* lives upon small Oligochætes. Their usual habitat is in the earth or in leaf mould: *Atherix*, however, is aquatic. The larva of *Xylophagus* differs from that of other Leptidæ in the head being prolonged into an elongate pointed process, which bears a small terminal opening, through which the mandibles are protruded. The thoracic and posterior abdominal segments have strongly chitinized dorsal areas, and two powerful anal hooks are evident. This curious larva is adapted for making its way through rotting wood and beneath bark, and is stated to be predaceous; it is figured by Verrall (1909), Perris (1870) and Malloch (1917). The larva of *Cœnomyia* has been described by Beling and also Malloch (1917): it exhibits affinities with that of *Xylophagus*, having somewhat similar chitinized dorsal areas. It occurs in decaying wood and in earth near trees. The larva of *Atherix* has been described by Dufour, Brauer, and more recently by Malloch (1917): the head is minute and each abdominal segment bears a pair of pseudopods capped by spines. The sides of the body are fringed with numerous filamentous processes which have been regarded as gills, no spiracles having been detected. The anal segment carries a pair of prominent, hairy, backwardly directed processes. The females of *Atherix* deposit their eggs in masses on dry twigs, etc., overhanging water, into which the larvæ fall upon hatching out. Many individuals lay their eggs on the same cluster, and afterwards die on the spot, often in numbers. As their dead bodies adhere together, large incrustations are thus formed. In Oregon the Indians at one time collected these masses of eggs and flies for food (Aldrich). Females of *Vermileo* lay their eggs in sand, and the larvæ construct conical pitfalls for the capture of their prey, after the manner of "ant lions." The 5th segment of the larva bears a ventral mobile pseudopod which assists in seizing and holding the prey. The 10th and 11th segments each carry a transverse row of long hooklets which serve as organs for boring and fixation.

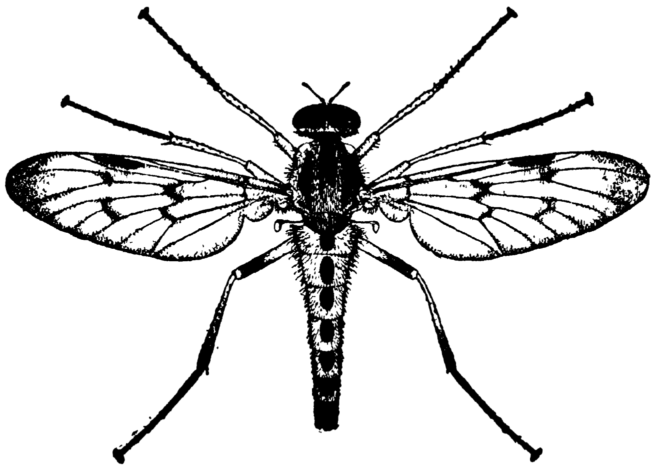

FIG. 599.—*LEPTIS SCOLOPACEA*, MALE. × 3. BRITAIN. *After* Verrall.

FAM. PANTOPTHALMIDÆ.—VERY LARGE BRISTLELESS FLIES WITH THE 3RD ANTENNAL JOINT ALWAYS ANNULATED. ANTERIOR VEINS NOT APPROXIMATED NEAR THE COSTA, C ENCOMPASSING THE WHOLE WING: SQUAMÆ ABSENT. MIDDLE TIBIÆ ONLY WITH A SPUR (RUDIMENTARY), PULVILLI AND AROLIUM PAD-LIKE.

A very small family consisting of about 20 species of relatively gigantic flies occurring in Central and South America and the West Indies. They are stated to inhabit forests, often alighting on tree trunks. The antennæ exhibit a remarkable sexual difference, an annulated flagellum being present in the female which, in the male, is much shorter and terminates in an arista. The eyes of the latter sex are holoptic, with enlarged facets on the frontal and upper regions. The proboscis is short and not adapted for piercing, and in the female there is a conspicuous several-jointed ovipositor. The larvæ have been found in the wood of trees and the metamorphoses of *Pantopthalmus* are described by Greene and Urich (*Trans. Ent. Soc.* 1931). They are thick-skinned, shortly cylindrical, with a small head and large prothoracic segment. The last segment is chitinized dorsally, and armed with a double series of hooklets and the spiracles are concealed by an overlying flap. The relations of the family appear to be with the Stratiomyidæ on the one hand, and with the Leptidæ and Tabanidæ on the other. For a general revision of the family, see Austen (1923).

FAM. TABANIDÆ (Horse Flies and Clegs).—BRISTLELESS FLIES OF STOUT BUILD WITH THE 3RD ANTENNAL JOINT ANNULATED BUT DEVOID OF A STYLE (Fig. 578). EYES

VERY LARGE, LATERALLY EXTENDED; PROBOSCIS PROJECTING, ADAPTED FOR PIERCING IN THE FEMALE (Fig. 580). SQUAMÆ LARGE, PULVILLI AND AROLIUM PAD-LIKE.

An extensive family of moderate to large sized flies (Fig. 600), including about 2,000 species, which are distributed over the whole world: 5 genera and 21 species are British. They are more or less flattened insects and, as a rule, mottled brown, tawny or grey in colour; *Chrysops*, however, has more conspicuous hues. During life the eyes are iridescent, exhibiting brilliant shades of green marked with bands or spots of brown or dark purple. In British Tabanids the proboscis is always rather short, but almost every transition may be found among the various genera of the family culminating in species of *Pangonia*, where it may be more than twice the length of the body.

Horse flies are active on warm sunny days, and the females are well-known blood-suckers, whereas the males mostly subsist upon honeydew and on the juices of flowers. In the absence of blood, the females will also imbibe these same substances (Hine). Many species are swift fliers, and those of *Tabanus* are particularly troublesome to horses and cattle, approaching their victims with a loud hum. The piercing action of the proboscis is often painful, but is seldom accompanied by inflammation. Experimental evidence indicates that the disease of horses known as Surra is transmitted by the punctures of *T. striatus*, and other species, and that these flies play an important part in spreading the infection. According to Leiper *Chrysops dimidiata* is a vector of *Filaria loa* which is responsible for the affection known as Calabar swellings among the natives of West Africa.

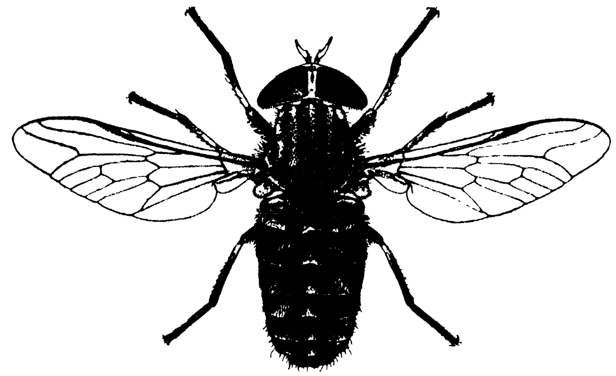

FIG. 600.—*Tabanus maculicornis*, FEMALE. × 3. BRITAIN.
After Verrall.

Pangonia may often be found hovering over flowers on the borders of forests; species have been observed to attack both man and cattle in various parts of the world. Their method of attack varies considerably in the experience of different observers. The labium is not adapted for piercing, the latter operation probably being performed by the other trophi, the proboscis only being used for sucking up the blood. In some species this is performed on the wing, in others it is stated to take place after the insect has alighted (Tetley, *Bull. Ent. Res.*, 1918). The species of *Hæmatopota* or "clegs" are voracious blood-suckers and especially frequent damp meadows. They are notable for their quietness of approach, and often the pricking sensation of their punctures is the first intimation of their presence. *H. pluvialis* is the most abundant English Tabanid, and is particularly troublesome to man. According to Portchinsky, in parts of Russia, these flies are so numerous and offensive that agricultural operations have to be carried out at night. By covering the pools frequented by Tabanids with a thin layer of petroleum he succeeded in destroying large numbers of these troublesome insects, which were killed by the oil adhering to their bodies.

The eggs of Tabanidæ are spindle-shaped and white, brown, or black; they are deposited in compact masses on the leaves and stems of plants, growing in water or marshy places. The larvæ (Fig. 597) are 12-segmented with a relatively small retractile head, well-developed antennæ and strong mouth-hooks. The trunk is cylindrical, tapering at both extremities, and usually longitudinally striated; there is a circle of prominent fleshy pseudopods around each of the first abdominal segments. They are metapneustic with the spiracles placed closely together in a vertical fissure at the anal end of the body. Near the hind extremity of the larva of *Tabanus* is a pyriform sac, narrowing posteriorly into a fine tube which opens at the surface between the last two segments. Within the sac is a series of capsules, each containing a pair of minute black pyriform bodies which are attached to the walls by means of delicate pedicels. The whole structure is known as *Graber's organ*, and can readily be seen through the integument of the living larva. It is well supplied by nerves and is presumably sensory in function. The larvæ of *Tabanus* and *Chrysops* are closely alike but according to Malloch (1917) in *Chrysops* the thoracic segments are either smooth, or less markedly striated than the abdominal, and the apical antennal joint is much longer than the one preceding. In *Tabanus* the striation is uniformly well developed over the body, and the terminal antennal joint is shorter than the preceding one The larva of *Goniops* differs from the usual Tabanid form in that the hindmost segments are stouter than those preceding thereby imparting to the body a pyriform or club-shaped appearance (McAtee, *Proc. Ent. Soc. Wash.*, 1911). The larva of *Hæmatopota* resembles that of *Tabanus* but according to Perris (1870) and Lundbeck (1907) it is amphipneustic.

Tabanid larvæ have been found in a variety of moist situations—in damp soi bordering ponds and streams, under stones in similar places, in mud, wet rotting logs etc. They are carnivorous, devouring small earthworms, crustacea and insect larvæ The pupæ are markedly elongate and cylindrical. They are characterized by the thoracic spiracles being connected subcutaneously with a large cavity on either side of the median line, near to the anterior margin of the thorax. Each abdominal segment carries 1–2 dorsal bands of closely contiguous setæ and a weaker series ventrally The terminal segment is armed with six stout pointed projections.

The literature on the family is considerable and for a general account, including the British species, consult Verrall (1909), Lundbeck (1907), and the work of Austen (1906). For the morphology and biology vide Cragg (1912) on *Hæmatopota*, the textbook of Patton and Cragg (1912) and the recent paper of Marchand (*Monog. Rockfeller Inst.*, 13).

FAM. CYRTIDÆ (Acroceridæ).—BRISTLELESS FLIES WITH THE HEAD VERY SMALL AND ALMOST ENTIRELY COMPOSED OF THE EYES WHICH ARE HOLOPTIC IN BOTH SEXES THORAX HUMPED, SQUAMÆ EXCEEDINGLY LARGE: ABDOMEN GREATLY INFLATED AND GLOBULAR. PULVILLI AND AROLIUM PAD-LIKE.

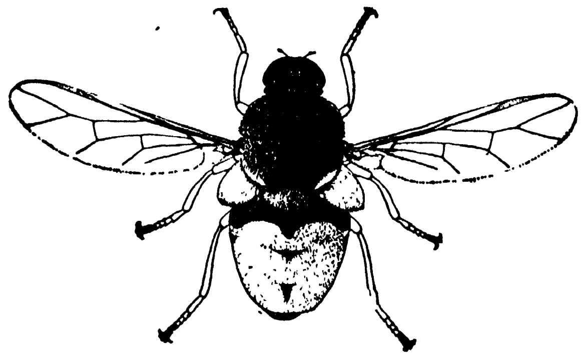

FIG. 601.—*Acrocera globulus*, MALE. × 7·5. BRITAIN.

After Verrall.

A small family of medium-sized flies including about 200 species which are readily distinguishable from all other Brachycera. Although occurring in all parts of the world Cyrtidæ are local and uncommon: two genera, *Oncodes* and *Acrocera* (Fig. 601) are found in the southern portion of England (Verrall, 1909). So far as known their larvæ are parasitic upon spiders living in the egg-cocoons or attached to the abdomen of their host. The eggs are black, and have been noted on dead twigs and on *Equisetum*: those of *Oncodes* are laid in masses (Maskell, *Trans. N.Z. Inst.*, 1888). The life-history of *Pterodontia* has been partially followed by King (1916). The newly-hatched larva bears a striking resemblance to the triungulin of *Stylops*: it is strongly chitinized, and armed dorsally and ventrally with segmental bands of powerful spines and pectinate scales. At the caudal extremity of the 8th abdominal segment is a sucker, which is flanked by a long anal seta on either side. In addition to a looping leech-like movement, the larva is able to leap by standing erect upon its sucker, with the caudal setæ bent beneath the body: a sudden straightening of the setæ lifts the larva 5 or 6 mm. in the air. The insect bores its way into the host by penetrating the articular membranes of the legs, and lives endoparasitically: according to King there are no spiracles. The older larvæ in this family are short and stout, and apparently amphipneustic: Konig (1894) and Maskell state that the younger larvæ, of presumably *Oncodes*, are metapneustic; they similarly possess leaping powers. According to Brauer (1869), the larva of *Astomella* lives within the abdomen of the spider, with its hind spiracles penetrating the lung-books of the latter. The pupæ in this family are devoid of spines or bristles, and differ from those of other Diptera in the great size of the thorax, which exceeds the abdomen in length.

FAM. NEMESTRINIDÆ.—RATHER LARGE BRISTLELESS FLIES WITH MANY OF THE VEINS RUNNING PARALLEL WITH THE HIND MARGIN OF THE WING: SC AND R_1 VERY LONG. THIRD ANTENNAL JOINT SIMPLE WITH A TERMINAL STYLE, PULVILLI AND AROLIUM PAD-LIKE BUT OFTEN MINUTE.

A family of about 150 species (Fig. 602), none of which occur in the British Isles and, according to Verrall (1909), only eight are European. They are for the most part inhabitants of hot and arid regions where there is a minimum of rainfall. They mainly frequent flowers, hovering over them while imbibing the nectar. The proboscis is very variable and often long, or very long; in *Nemestrina longirostris* it is about four times the whole length of the insect.

The larvæ of this family have a very small retractile head and 12 trunk segments; the tracheal system is amphipneustic, with the posterior spiracles spaced apart in a transverse fissure. The life-history of *Hirmoneura* has been partially observed by Brauer (*SB. Akad. Wein.*, 88) and Handlirsch (*Wein. Ent. Zeit.*, 1882). Its habits resemble to some extent those of the Bombylidæ and hypermetamorphosis also occurs. The young larva is slender and provided with a pair of pseudopods on the 6th and 12th segments, which are not present at a later stage. It appears that this species is parasitic upon *Rhizotrogus solstitialis*, and probably upon other Coleoptera. The eggs are deposited in clusters within the burrows of Coleoptera (other than *Rhizotrogus*) from whence the newly-hatched larvæ issue in large numbers. They are stated to place themselves in an erect position by means of their terminal hooklets, and are blown away by the wind. Their subsequent history is unknown, but it is believed that they attach themselves to the body of the female *Rhizotrogus*, and are thus carried to the place in the earth where the latter lays her eggs.

FAM. APIOCERIDÆ.—RATHER LARGE ELONGATE BRISTLY FLIES: ANTENNÆ WITH OR WITHOUT A SHORT STYLE, PALPI SPATULATE. VENATION RATHER SIMILAR TO MYDAIDÆ, M_1 TERMINATING BEFORE WING APEX. TWO PULVILLI ARE PRESENT AND THE AROLIUM IS WANTING OR BRISTLE-LIKE.

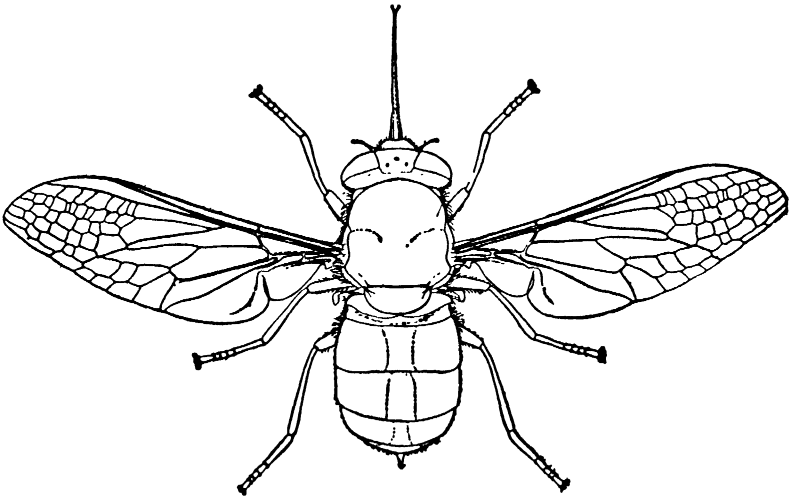

FIG. 602.—*NEMESTRINA PEREZI*, FEMALE. × 3·25.
After Verrall.

A very small family comprising about 30 species, none of which are European. They are thickly pilose insects with a non-piercing proboscis; their life-history has not been investigated.

FAM. MYDAIDÆ.—VERY LARGE FLIES DEVOID OF BRISTLES AND OBVIOUS PUBESCENCE. ANTENNÆ TERMINATING IN A JOINTED AND USUALLY CLUBBED STYLE. VENATION COMPLEX; R_1 VERY LONG RECEIVING SEVERAL SUCCEEDING VEINS BEFORE ITS APEX, R_4, R_5 AND M_{1+2} BENT FORWARDS TOWARDS THE APEX OF THE WING. PULVILLI MODERATELY LARGE, NO EMPODIUM.

A family of mostly exotic forms with a few moderate-sized species occurring in Southern Europe. It includes the largest known Diptera, and the adults are stated to be predaceous, but only very scanty observations are available. The larvæ have been found in decaying wood and, in some cases, are known to be predaceous upon coleopterous larvæ.

FAM. SCENOPINIDÆ (Omphralidæ).—NARROW OBLONG FLIES DEVOID OF TRUE PUBESCENCE OR BRISTLES. FIRST TWO ANTENNAL JOINTS SHORT, THE THIRD ELONGATE AND DEVOID OF A STYLE OR ARISTA. VEIN M_{1+2} TERMINATING BEFORE THE APEX OF THE WING, R_1 SHORT. PULVILLI SMALL, EMPODIUM BRISTLE-LIKE.

This family includes rather small dark coloured flies and scarcely 50 species are known. The adults are occasionally found on windows, or about stables and outbuildings. The larva of *Scenopinus* (vide Perris, 1870) resembles that of *Thereva.* It is amphipneustic, white and vermiform, with serpent-like movements. The head is brown and well-developed, and is followed by 20 apparent segments. Most of the abdominal somites are subdivided by a strongly marked constriction, thus giving the appearance of an increased number of segments: the terminal segment bears two small styles. At one time it was believed that these larvæ fed upon neglected carpets, horse-rugs, etc.: there is little doubt, however, that they are predaceous upon the larvæ of *Tinea pellionella* and of other insects. Scenopinid larvæ have also been found in *Polyporus,* in branches of trees, and other situations.

FAM. ASILIDÆ (Robber Flies).—USUALLY ELONGATE BRISTLY FLIES WITH A HORNY PROBOSCIS ADAPTED FOR PIERCING, AND THE PALPI NEVER SPATULATE. VEIN R_1 VERY LONG, M_1 TERMINATING SOME DISTANCE BEYOND THE APEX OF THE WING. LEGS POWERFUL AND PREHENSILE: PULVILLI LARGE, EMPODIUM BRISTLE-LIKE.

The Asilidæ are moderate to very large sized flies (Fig. 603), always bristly, and in *Laphria* also densely hairy. They constitute the largest family of Brachycera, numbering at least 3,000 species: in the British Isles 23 species are recognized by Verrall (1909). The adults are predaceous in habit, their powerful legs being adapted for grasping the prey. The proboscis is firm and horny, directed downwards or obliquely forward. A prominent tuft of hairs, forming a "mouth beard," and the protuberant eyes are characteristic of the family. The conspicuous male genitalia and the corneous ovipositor are also well marked features.

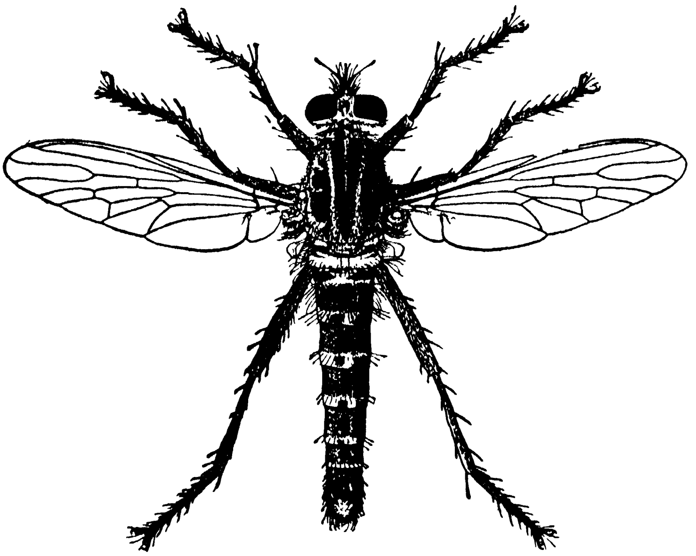

FIG. 603.—*Philonicus albiceps*, Male. × 3. Britain. *After* Verrall.

The prey of Asilidæ is extremely varied and information on the subject has been collected by Whitfield (1925). It appears that the females are far more commonly found with prey than the males; it is remarkable, as Poulton adds, that the stings of Aculeates, the distasteful properties of the Danainæ, Acræinæ, and of the odoriferous *Lagria,* the hard chitin of Coleoptera, and the aggressive powers of the Odonata are alike insufficient protection against these voracious insects. Whether Asilids inject any poison into their victims or not has yet to be ascertained. It has been recorded that the captured insect collapses very rapidly after being perforated by the proboscis, which suggests that some toxic secretion may be present.

Asilid larvæ live in soil, sand, wood, or in leaf-mould, and are either predaceous or scavengers. They are cylindrical with a small, dark coloured, pointed head and are amphipneustic, the spiracles being situated on the prothoracic and penultimate segments. The mouth-parts comprise a hook-shaped labrum, knife-like mandibles, and large broad maxillæ with 2-jointed palpi. Small papilla-like antennæ are present, but no eyes. The anterior abdominal segments are provided either with ventral intersegmental areas, or circlets of pseudopods (*Laphria*) resembling those of Tabanid larvæ. Ten or eleven segments are present, the higher number depending upon whether a short and indistinct segment-like swelling at the anal extremity is regarded as a true somite or not. The pupæ are remarkably spined about the head: the abdominal segments have a dorsal girdle of spines, a ventral girdle of bristles, and the apex of the abdomen also bears spinous projections. The larva of *Laphria* has been found beneath bark and in the burrows of Longicorn larvæ living in *Pinus*: it has been figured by Perris (1870) and later by Sharp (vide Verrall, 1909). For the metamorphoses of other genera vide Melin (1923) and Lundbeck.

FAM. THEREVIDÆ.—MORE OR LESS ELONGATE DENSELY PUBESCENT FLIES

WITH SLENDER NON-PREHENSILE LEGS. THIRD ANTENNAL JOINT WITH AN APICAL (SOMETIMES JOINTED) STYLE. R_1 USUALLY LONG, CELL M_3 PRESENT. EMPODIUM ABSENT, OR REPRESENTED BY A WEAK BRISTLE.

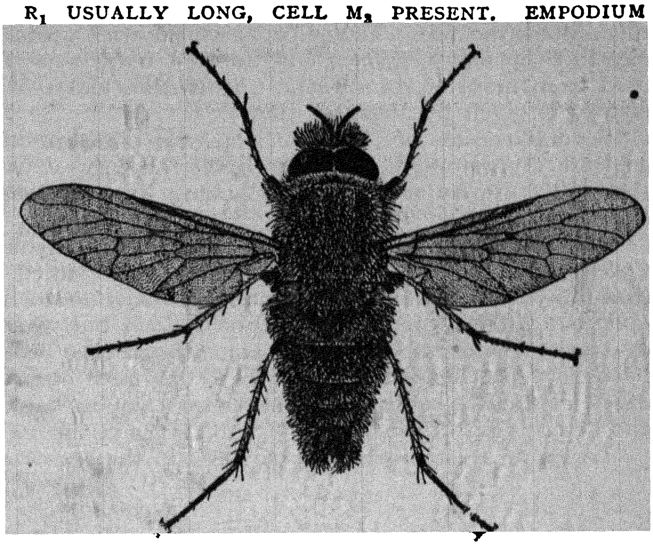

FIG. 604.—*Thereva nobilitata*, MALE. × 4. BRITAIN. *After* Verrall.

A small family including about 300 described species (Fig. 604) of which about a dozen are British. They exhibit a resemblance to some Asilidæ, but the weaker legs and the non-protuberant eyes enable them to be readily separated. In habits these flies are commonly stated to be predaceous, but very few direct observations appear to have been made. The proboscis is rather prominent, and provided with fleshy labella, instead of the horny apex as in the Asilidæ. The larvæ (Fig. 605) of several species are known to be predaceous upon those of other insects, including wireworms, etc. They live in the soil, among leaf mould, in fungi, decaying wood, etc., and exhibit quick serpent-like movements. They are smooth and vermiform, bearing an extremely close resemblance to the larvæ of *Scenopinus* (vide p. 658). The larva of *Thereva* (Malloch, 1915B) has a small though distinct head, followed by 20 segment-like divisions. The labrum is hook-like, and the mandibles also exhibit a hooked form: small antennal papillæ are present but no eyes. A pair of prominent latero-ventral bristles are found on each thoracic segment, and three pairs of bristles on the 10th abdominal segment: the tracheal system is amphipneustic. At the anal extremity are two small styliform processes. The pupa has thorn-like, projecting antennæ and a long curved spine at the base of each wing.

FAM. BOMBYLIIDÆ (Bee Flies).—DENSELY PUBESCENT WITH ELONGATE SLENDER LEGS, AND OFTEN A LONG PROJECTING PROBOSCIS. THIRD ANTENNAL JOINT SIMPLE, STYLE SMALL OR VESTIGIAL, AND NOT MORE THAN 2-JOINTED (Fig. 578). CELL M_3 ABSENT. PULVILLI SOMETIMES AND AN EMPODIUM ALWAYS RUDIMENTARY.

Most of the flies of this family are moderate or rather large in size and, although often bearing bristles, the latter are hidden by the dense pubescence (Fig. 606). The proboscis is usually very long and projecting forwards, but is sometimes short with broad labella. The wings are often darkly marbled and, when at rest, they remain half opened or outspread. Although only 9 species frequent Britain probably considerably over 2,000 are known.

The larvæ are parasites and when young, they are elongate and slender, with a very small head, and 12 trunk segments. They are stated to be metapneustic; each thoracic segment bears a pair of long setæ, and a further pair is carried at the anal extremity. They undergo hyper-metamorphosis and, when fully grown, are cylindrical or somewhat flattened, with a small retractile head and no eyes: the spiracles are found on the prothoracic and penultimate segments. The pupæ are very characteristically spined on the head, with bands of hooklets across the dorsal side of the abdomen.

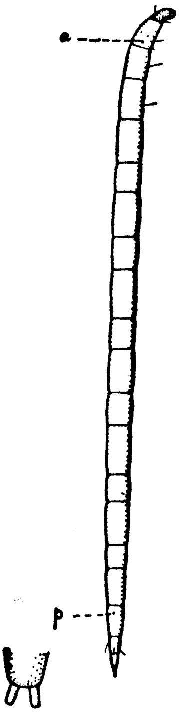

FIG. 605.—LARVA OF *Thereva* AND ANAL SEGMENT MORE ENLARGED. *a*, anterior and *p*, posterior spiracles.

The larvæ of *Argyramœba* Schin. are parasites on those of solitary bees and fossorial wasps. The life-history of *A. trifasciata* Mg. has been observed by Fabre

(*Souv. Entom.*, 3). The eggs are deposited on the ground, near the nest of the host (*Chalicodoma muraria*), and it appears that the young larva has to make its way into the cell of the bee. The pupa is armed with cephalic spines for the purpose of piercing the masonry enclosing its host. *Argyramœba anthrax* (*sinuata*) has been bred from nests of *Anthophora, Chalicodoma* and *Osmia* and an account of its life-history is given by Verhoeff (1891).

Several species of *Anthrax* Scop. are parasitic upon Noctuid larvæ or pupæ, aculeate Hymenoptera, and also upon the eggs of Orthoptera. Other members of the genus are hyperparasites attacking hymenopterous or dipterous parasites of Lepidoptera.

The larvæ of *Bombylius* L. are parasitic upon solitary bees (*Andrena, Halictus, Colletes*, etc.): those of *B. minor* have been studied by Nielsen (1906) who states that the young larva is very like that of *Argyramœba* in form. At this stage it feeds upon the pollen stored in the cell of *Colletes*, but when it attains a length of 2 mm. it attacks its host larva: it subsequently moults, becoming maggot-like and amphipneustic. The life-history of *B. major* has been observed by Chapman (*Ent. Month. Mag.*, 1878): the eggs were deposited on a sloping bank while the fly was on the wing, and descriptions of the larva and pupa agree in the main with those of *B. minor.*

Larvæ of *Systœchus* live as parasites in the egg-cases of the locusts *Œdopoda* and *Stauronotus*: the larva and pupa of *S. oreas* are described and figured by Riley (1880). According to Künckel d'Herculais (1905) the larva of *Systropus* parasitizes larvæ of the Lepidopteron *Limacodes*. *Spogostylum* is parasitic upon *Xylocopa*, and other bees, and is also recorded from two genera of Coleoptera: for the life-history of *S. anale* Say., a parasite of Cincindelid larvæ, vide Shelford (1913).

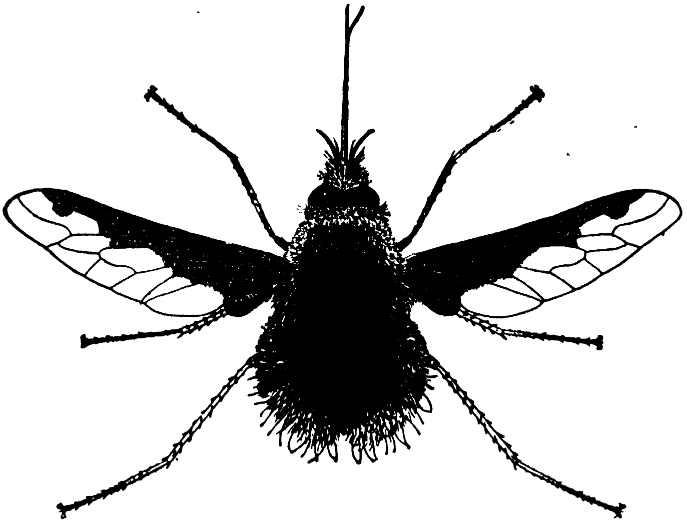

FIG. 606.—*BOMBYLIUS MAJOR*, MALE. × 3. BRITAIN. *After* Verrall.

FAM. EMPIDÆ.—BRISTLY FLIES WITH A HORNY PROBOSCIS ADAPTED FOR PIERCING; THE STYLE OR ARISTA (IF PRESENT) ALMOST ALWAYS TERMINAL. CELLS M AND 1ST M_2 SEPARATE, CELL CU GENERALLY SHORT. EMPODIUM LINEAR—MEMBRANOUS, OR SETIFORM.

A family of medium to very small sized flies of grey, yellowish, or dark coloration, very rarely metallic. About 1,600 species are known, and in Britain there are over 200 representatives. The proboscis is of variable length, and is generally rigid and downwardly projecting. The legs often display sexual characters, the male exhibiting special structural features such as thickened femora, tibiæ or tarsi (Fig. 607). Empidæ may be distinguished from the Asilidæ by the absence of the face-beard and the much shorter cubital cell. Their species are predaceous upon smaller insects and, according to Poulton (1906), they prey most frequently upon Diptera; in this feature they are sharply contrasted with the Asilidæ.

Species of *Empis*, *Hilara* and *Rhamphomyia* may often be observed "dancing" or swarming in the air after the manner of Chironomids—a behaviour which is concerned with the meeting of the sexes. Either one or both sexes may perform these aerial evolutions and, in many species of the above genera, the males catch the prey, and kill but do not devour it. On meeting a female the latter receives the prey and feeds upon it during coitus: when copulation is accomplished the female drops the prey. The true significance of this remarkable habit is not understood (vide Hamm, *Ent. Month. Mag.*, 1909). An American species, *Empis aerobatica*, makes a curious frothy balloon, enclosing a small prey, which is probably transferred to the female during copulation; it is often released after the latter function is accomplished.

Species of *Hilara* envelop their prey in a slight web before offering it to the female: the web is constructed by the male from a secretion of glands opening on the fore tarsi (Eltringham, 1928). *H. sartor* Beck. constructs a more extensive web than other species, and a whole literature has grown up around the subject of the origin and significance of this structure (vide Wheeler, *Journ. Heredity*, 1924, p. 491).

Larval Empidæ are cylindrical, more or less spindle-shaped, with a very small retractile head and 11 trunk segments. They are amphipneustic, and most of the abdominal segments are provided with transverse ventral swellings, or more strongly developed pseudopods. The anal segment is somewhat rounded, and provided with a small terminal protuberance or spine, above which lie the posterior spiracles. Empid larvæ live in soil or among leaves and humus, in decaying wood, among moss, etc.: a few, such as *Hemerodromia*, are aquatic. Only scanty observations have been made with regard to their feeding habits but, in a few cases, they have been found to be carnivorous. The larvæ of several genera are briefly described by Beling (1882, 1888); the metamorphosis of *Hemerodromia* is dealt with by Brocher (*Ann. Biol. lacus.*, 1901) and that of *Rœderoides* by Needham and Betten (1901). Kieffer (1900) has described the larva and pupa of *Empis meridionalis* and Brauer (1883) figures the larva of *Hilara lurida*.

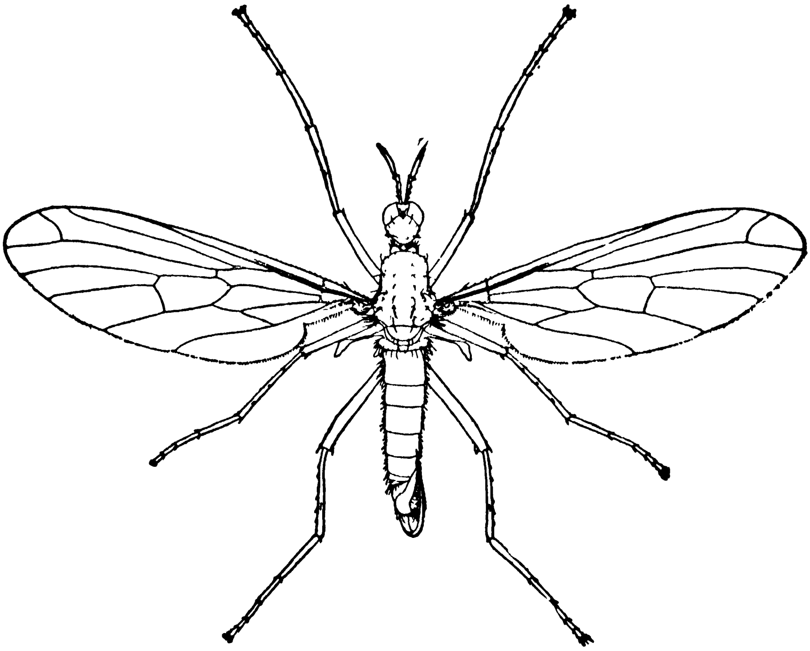

FIG. 607.—*EMPIS TRIGRAMMA*, MALE. × 6. BRITAIN.
After Verrall.

FAM. DOLICHOPODIDÆ.—SMALL BRISTLY METALLIC GREEN OR BLUE-GREEN FLIES WITH A DORSAL OR TERMINAL ARISTA, AND A SHORT FLESHY PROBOSCIS. CELLS M AND 1ST M_2 CONFLUENT, CELL CU VERY SHORT. TWO PULVILLI AND A LINEAR, OR NARROWLY LOBIFORM, AROLIUM.

A large family comprising more than 1,400 species of which nearly 200 are British (Fig. 608). The various species occur among grass and low herbage, generally in damp situations; several genera frequent the sea-shore.

The venation of the family is very similar to that of the *Ephydridæ*, which certain species also resemble in their behaviour and habitat. The secondary sexual characters in the males attain a remarkable degree of development and may affect almost any of the outer parts of the body.

In adult life the Dolichopodidæ are predaceous upon minute soft-bodied insects, etc., which they envelop by means of the labella while extracting the juices. According to Becker (1882) some amount of mastication of the prey takes place on account of the mobility of the labrum during feeding. In America, according to Malloch, many species occur on flowers and undoubtedly feed upon nectar. It is likely that both habits are of frequent occurrence, though further observations are needed.

The larvæ of this family have been found in a variety of situations and live beneath the ground, in rotten wood, among humus, etc., while others are aquatic. In *Aphrosylus* the larva lives among cast-up weed on the sea-shore, while those of several species of *Medeterus* prey upon the larvæ and pupæ of wood-boring Coleoptera. Most of the larvæ of this family are probably carnivorous. They are elongate and cylindrical, 12-segmented, with a small retractile head, and most of the abdominal segments bear pseudopods armed with locomotory spinules. The last segment is obliquely truncated, often slightly swollen, and carries four short protuberances. The tracheal system is amphipneustic, and both pairs of spiracles are small: exceptions are met with in *Medeterus* (peripneustic) and *Argyra* (metapneustic).

The pupæ are, as a rule, short and stout with a pair of elongate thoracic respiratory horns. Lundbeck states that larva of *Dolichopus* forms an earthen pupal cell, lining the interior thereof with a secretion forming a dense film-like layer. At one extremity the latter is wanting over a smaller area through which the pupal horns protrude. As the cocoon is apparently impenetrable to air Lundbeck thus explains the significance of the long pupal horns, so characteristic of the family. In other cases the cocoon is constructed of wood fragments, etc., and is lined by silken material. Although the metamorphoses of a number of species have been described the life-history has rarely been followed in any detail. Marchand (*Ent. News*, 1918) has described the larva and pupa of *Argyra*, Perris (1870) those of *Medeterus*, and *Thrypticus* has been studied by Johannsen and Crosby (*Psyche*, 1913) and also by Lubben (1908).

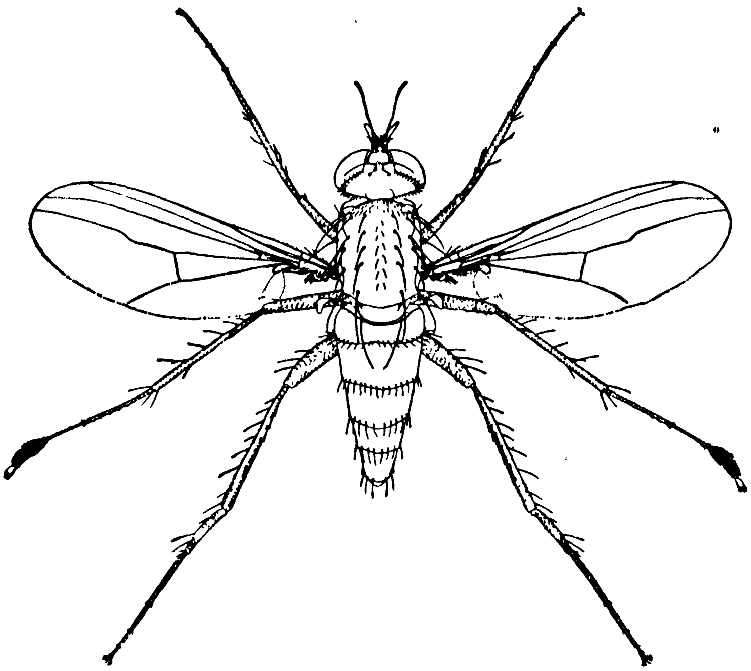

FIG. 608.—*DOLICHOPUS POPULARIS*, MALE. × 7·5. BRITAIN.
After Verrall.

Sub-order III. **Cyclorrhapha**

The Cyclorrhapha are divided into three sections as given below:

Section A. ASCHIZA

Frontal suture obscure or restricted: lunule often indistinct or absent: ptilinum always absent. Cell Cu elongated (except in Phoridæ) and extending more than half-way to wing margin.

Section B. SCHIZOPHORA

Frontal suture and lunule distinct: ptilinum always present. Cell Cu short or vestigial (except in Conopidæ).

Section C. PUPIPARA

Head closely united with thorax or folded back on same. Usually flattened flies, with leathery or horny integument, adapted for ectoparasitic life on warm-blooded vertebrates. Ptilinum present or absent: wings often reduced or wanting. Viviparous; larvæ extruded when about to pupate.

Section A. ASCHIZA

FAM. LONCHOPTERIDÆ (Musidoridæ).—THIRD ANTENNAL JOINT ROUNDED OR GLOBULAR WITH A LONG TERMINAL OR SUB-DORSAL ARISTA. WINGS POINTED AT THE APEX AND WITH NO OBVIOUS CROSS VEINS, R_S WITH ITS TWO BRANCHES CLOSELY APPROXIMATED AT THE WING APEX. EMPODIUM WANTING.

This family includes a few small, slender, bristly flies, usually pale coloured, and often found along the borders of shady streams. The larvæ of *Lonchoptera* have been found among leaves and other vegetable matter. According to de Meijere (1900) they are amphipneustic, much flattened and with long anterior and posterior setæ. The head is vestigial and there are only 10 apparent trunk segments, of which the last appears to be of a composite nature, and bears a pair of widely separated spiracles (Fig. 609).

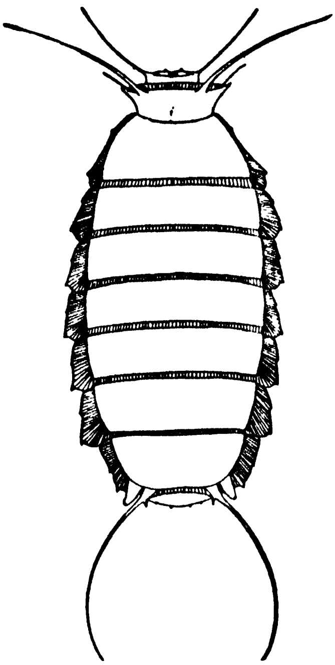

Fig. 609.—Larva of *Lonchoptera*; Magnified. Britain.

FAM. PHORIDÆ.—ANTENNÆ APPARENTLY CONSISTING OF ONE LARGE JOINT, WHICH CONCEALS THE OTHERS, AND BEARING A LONG APICAL OR SUB-DORSAL ARISTA. WINGS OFTEN VESTIGIAL OR ABSENT. ANTERIOR VEINS VERY HEAVILY DEVELOPED, AND JOINING COSTA ALONG THE PROXIMAL HALF OF THE LATTER: REMAINING VEINS WEAK AND ABNORMALLY DISTRIBUTED.

A family of small or minute greyish-black or yellowish flies (Fig. 610): they are active runners and present a curious humped appearance. Their habits are varied but the adults are frequently met with among decaying vegetation, while others occur in the nests of ants and termites. The wings exhibit a wide range of variation as regards degree of development, especially among the females; certain apterous and micropterous genera are only known from that sex. In *Ecitomyia* (female) for example, the wings are narrow and strap-like, and in *Puliciphora* (female) they are totally wanting.

The affinities of Phoridæ have been more frequently discussed than perhaps any other family of Diptera (Brues, 1907); some authorities place them at the end of the Brachycera while others regard their true position as being among the Cyclorrhapha—a conclusion which is supported by their metamorphoses.

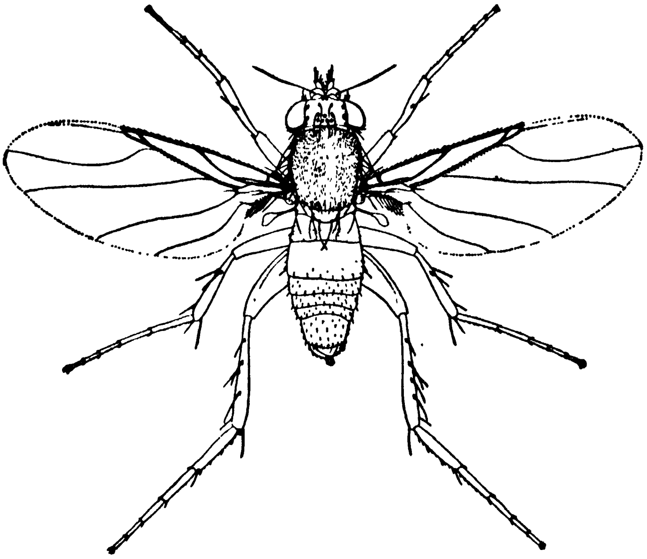

Fig. 610.—*Phora urbana*, Male. × 10. Britain. *After* Verrall.

The larvæ of *Phora* (vide Keilin, 1911) live in decaying vegetable matter and dead animals, especially *Helix* (Schmitz, 1917): others are mymecophilous and some are parasites. They resemble those of other Athericera in their general morphology and consist of a reduced head, 3 thoracic and 8 abdominal segments. Furthermore, they agree with this sub-order in being metapneustic in the 1st instar and amphipneustic subsequently. Each segment bears metamerically arranged bands of papillæ. Pupation takes place in the larval skin, and the pupa carries a pair of elongate processes on the 2nd abdominal segment, which appear as the anterior respiratory horns on the puparium.

One of the most remarkable of all Phoridæ is *Termitoxenia* which has the wings reduced to minute vestiges and inhabits termites' nests: according to Wasmann (1900) it has lost its larval and pupal stages and is consequently ametabolic. This observer concludes that it is hermaphrodite and the same individual becomes successively male and female. There are, furthermore, two types of individuals present—stenogastric and physogastric. In the former the chitin is extremely soft and the abdomen retracted: in the latter chitinization is normal, but the abdomen is greatly enlarged and swollen. Neither ametaboly nor hermaphroditism are proven, and Bugnion (1913) only found female organs present in *T. peradeniyæ*. A sperma theca containing a spermatophore is evident, and it is possible that this organ has been mistaken for a testis by Wasmann (1900) and Assmuth (1910). In *Puliciphora* de Meijere (1912) has found stenogastric and physogastric individuals, along with larval and pupal stages. On the other hand, according to Schmitz (1917) *Wandolleckia* is ametabolic, and has both types of individuals present: it is presumed to be a proterandric hermaphrodite. It is evident, therefore, that renewed investigation of these remarkable genera is greatly needed. As Keilin remarks (1919), the only way to prove that proterandric hermaphroditism exists is the discovery of spermatogenesis in the stenogastric forms. *Thaumatoxenia* is probably the most highly modified of all Phoridæ (vide Trägårdh, 1908: Borner, 1908): originally regarded as belonging to the Hemiptera, further study has shown that it is a Dipterous insect.

FAM. PLATYPEZIDÆ.—SMALL THINLY PILOSE FLIES WITH THE HIND TARSI REMARKABLY DILATED. THIRD ANTENNAL JOINT ELONGATE AND OFTEN PYRIFORM, ARISTA TERMINAL. CELL R_5 OPEN.

A small family including about 70 species of which less than a score are British (Verrall, 1901). They are usually to be met with dancing in the air in companies or running over herbage. Their most striking feature is afforded by the hind tarsi whose basal three or four joints are dilated, flattened, or ornamented in a curious manner, and very different in the male from the female.

An account of metamorphosis of *Callimyia* is given by de Meijere (1900); Willard (*Psyche*, 1914) also figures the larva and pupa of *Platypeza agarici* Will. The larvæ are broad and flattened with the sides bordered by long setæ: in *Callimyia* the whole margin is deeply incised, each incisure being strongly serrated. The trunk comprises 10 or 11 segments, the head and first segment being wholly ventral. The tracheal system is amphipneustic, with the anterior spiracles placed beneath the body; the posterior pair is inconspicuous and rather widely separated. So far as known the larvæ live in Agaracini.

FAM. PIPUNCULIDÆ.—THINLY PILOSE OR ALMOST BARE FLIES WITH A VERY LARGE SUBHEMISPHERICAL MOBILE HEAD FORMED ALMOST ENTIRELY OF THE EYES. ANTENNÆ WITH A USUALLY LONG DORSAL ARISTA. WINGS MUCH LONGER THAN THE ABDOMEN, CELL R_5 OPEN; TIBIÆ DEVOID OF SPURS. OVIPOSITOR HORNY, EXSERTED.

A very distinct family of small dark flies, the great majority of which pertain to the genus *Pipunculus*. They have a markedly hovering habit, and are usually to be taken on flowers, or by sweeping miscellaneous herbage. Their most striking feature is the great size and mobility of the head; the third antennal joint is of peculiar shape, being sometimes prolonged into a curious beak-like process. For general information on the family the reader is referred to the works of Perkins (1905) and Verrall (1901).

The larvæ are endoparasites of other insects, mainly Homoptera. They are narrowed anteriorly, and capable of a good deal of extension and retraction: segmentation is obscure but apparently 10 or 11 somites are present. The anterior spiracles are small, and situated a short distance behind the mouth; the posterior pair is dark coloured, approximated, and placed some distance in front of the anal extremity. The puparium is provided with a pair of anterior spiracular tubercles, while the posterior spiracles are very much as in the larva. Dehiscence of the puparium usually occurs by the detachment of the dorsal plate through which the spiracular horns project. The head of the larval parasite is directed towards that of the host, and the fully grown parasite fills the greater part of the abdomen of the latter. In certain cases it has been found that "castration parasitaire" results, and the abdomen of the female host is stated to undergo structural modification (vide Giard, *Comp. Rend.*, 1889; Keilin and Thompson, *C.R. Soc. Biol. Paris*, 1915), but further research is greatly needed. When the Pipunculid larva quits its host, it usually escapes at the junction of the metathorax and abdomen, either above or below, the segments being ruptured at that point. It falls to the ground and buries itself beneath the soil or among rubbish, etc.

FAM. SYRPHIDÆ (Hover Flies).—MODERATE TO LARGE SIZED FLIES WITH

BRIGHTLY COLOURED MARKINGS, ALMOST ALWAYS BRISTLELESS. ARISTA, WITH FEW EXCEPTIONS, DORSAL. CERTAIN OF THE VEINS FORMING A KIND OF SECONDARY MARGIN PARALLEL WITH THE OUTER WING-MARGIN ; CELL R_5 CLOSED ; VENA SPURIA PRESENT BETWEEN R AND M.

The Syrphidæ are one of the largest and most sharply defined families of Diptera. They are usually very brightly coloured flies and may be striped, spotted or banded with yellow on a blue, black, or metallic ground-colour. The black and yellow coloration often imparts to them a superficial resemblance to wasps : other species are densely hairy and resemble bumble-bees. Nearly all members of this family are attracted to flowers and may frequently be observed poised in the air, their wings vibrating with extreme rapidity, hence the name of " hover flies." The vena spuria (Fig. 612) is one of their most characteristic features and is found in no other family of Diptera. It is a vein-like thickening of the wing membrane and may be distinguished from true veins in being fainter, and terminating without association with other veins.

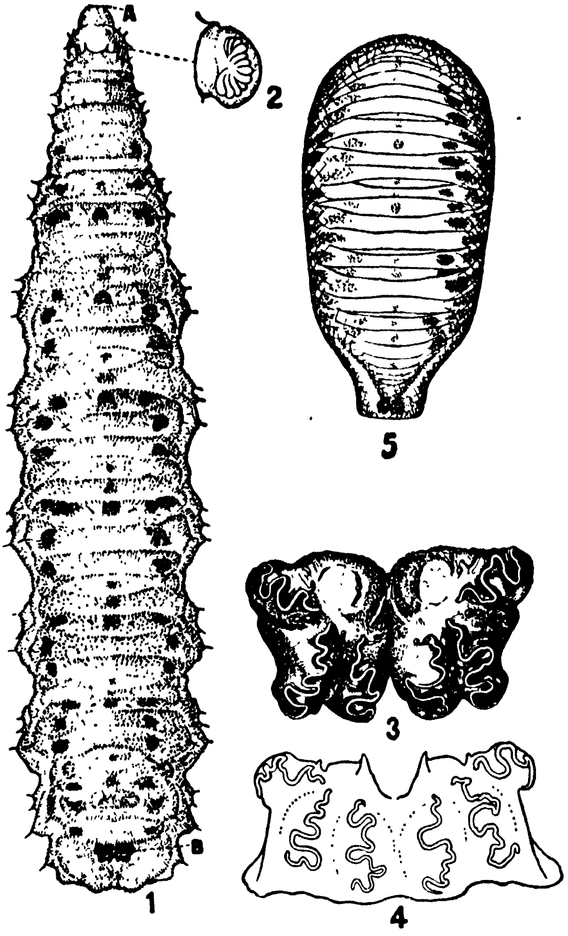

FIG. 611.—*Syrphus nitens.*

1, Larva × 7·5 ; A, antenna ; B, posterior respiratory organ. 2, Anterior spiracle more enlarged. 3, End view of posterior respiratory organ × 75. 4, Postero-ventral view of same × 75. 5, Puparium, dorsal view × 7·5. Adapted from Metcalf. *Bull.* 253 *Maine Agric. Exp. Sta.*

The larval habits of Syrphidæ are extremely varied. They may be: (*a*) *Phytophagous*, feeding externally upon plants (*Mesogramma polita*) or internally in bulbs (*Merodon equestris, Eumerus strigatus*), or within stems or in fungi (*Chilosia*). (*b*) *Carnivorous*, living predaceously upon aphids and the nymphs of other Homoptera (species of *Pipiza, Paragus, Melanostoma, Baccha, Syrphus*, etc). (*c*) *Saprophagous*, living in decaying organic material, dung, liquid mud, or dirty water (species of *Eristalis, Helophilus, Platychirus, Sericomyia, Syritta, Tropidia*, etc.) ; in the sap and wet, rotting wood of diseased parts of trees (*Xylota, Mallota, Myriatropa, Myiolepta, Ceria*, etc.). or as scavengers in the nests of ants and termites (*Microdon*) or of Aculeate Hymenoptera (*Volucella*). Verrall remarks that probably all the European species of *Volucella* are scavengers in the nests of large Aculeates, feeding upon diseased larvæ or pupæ, etc. : so far as known they are not predaceous and the association is consequently friendly and not resented by the hosts. *Volucella bombylans* occurs in the nests of *Bombus* while the species *zonaria, pellucens* and *inanis* are found in the nests of *Vespa*.

Morphologically, Syrphid larvæ (Fig. 611) may be recognized by the following characters. The head is greatly reduced and carries a pair of short fleshy, sensory processes. The cuticle is tough or leathery, and segmentation is obscure owing to the transverse corrugation of the body, but apparently 11 somites are present. The tracheal system is amphipneustic with the anterior spiracles on the 2nd apparent segment : the posterior pair is situated on two tubes of very variable length, which are fused together down the median line.

Three principal types of Syrphid larvæ may be recognized. 1. The aphidivorous type with the ventral aspect flattened, the body much attenuated anteriorly, and the posterior respiratory tubes very short. The body is frequently marked with green or brown, and the general appearance is rather slug-like ; all have a marked capacity for changing their shape (*Syrphus*, *Melanostoma*, etc.). 2. The short-tailed filth-inhabiting type with the body cylindrical and not attenuated anteriorly, and the respiratory tubes short. Three pairs of lateral fleshy protuberances are present on the 11th segment, and groups of branched plumose hairs are placed around the hind spiracles (*Syritta*, *Tropidia*, etc.). 3. The rat-tailed type with the body terminating in a long flexible respiratory process which, in some species, is capable of being extended several times the length of the body (*Eristalis*, *Helophilus*, etc.).

In addition to the above three types there are several anomalous larvæ. That of *Microdon* is broadly ovoid in outline and flattened ventrally, and is bordered by a row of marginal spines. The dorsal surface is convex and there is no evident segmentation or anterior spiracles. In general appearance it is slug-like and, when first described, it was regarded as a new genus of land Mollusca. This curious larva has been studied in detail by Cerfontaine (1907) and others. In the boring larva of *Merodon equestris* Fab. the body is cylindrical and much contracted, with rounded extremities: it comes nearest to type 2, but there are no fleshy protuberances on the 11th segment. In *Volucella bombylans* the larva is rather broad and fleshy, tapering anteriorly. The body is provided with numerous small lateral spinous outgrowths and larger terminal processes on the last segment (Künckel d'Herculais, 1875).

Prior to pupation Syrphid larvæ come to rest in some suitable place on, or near, their habitat. In many species the caudal segments are cemented to a leaf, twig or other support with a secretion apparently derived from the hind-gut; in other cases the larva buries itself in the soil or other medium. The puparium, as a rule, is considerably inflated dorsally and laterally: spiracles are present on the puparium in the region of the 4th or 5th larval segment and may be either sessile (*Melanostoma*) or elevated upon conspicuous horns (*Volucella*, *Eristalis*). Eclosion of the imago usually takes place by means of a dorsal rupture of the puparium and is therefore different from what obtains in almost all other Cyclorrhapha. A good deal of information concerning the structure and biology of Syrphid larvæ will be found in the writings of Metcalf (1916–17) and Krueger. The internal anatomy of both the larva and imago is dealt with by Künckel d'Herculais (1875) in his monograph on *Volucella*. The larva of *Eristalis* is described by Miall (1895) and Batelli (1879) and its tracheal system has been studied in detail by Wahl (1889).

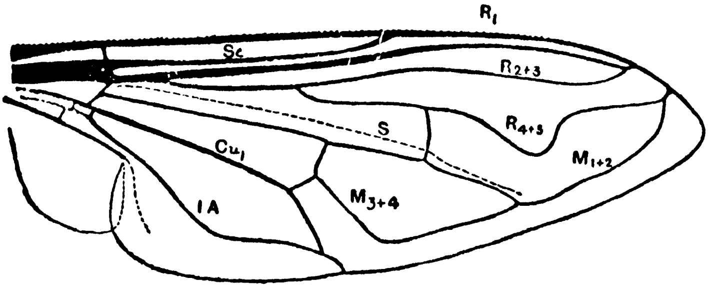

FIG. 612.—VENATION OF *ERISTALIS*.
s, vena spuria.

Economically, the predaceous larvæ of this family are notable in being important enemies of Aphididæ, Coccidæ and other Homoptera. The capacity of Syrphid larvæ for the rapid destruction of aphids is remarkable and Metcalf states that a larva of *Syrphus nitens*, which had not been fasting previously, caught and destroyed 21 examples of the large Aphid *Pterocomma flocculosa* in 20 minutes. The entire insect is never devoured, but only the soft and readily assimilated body-contents are sucked out. Notwithstanding the great size of the family, and its varied larval habits, very few Syrphids are in any sense injurious to man. The "Corn-feeding Syrphid Fly," *Mesogramma polita*, occurs in several states of N. America where its attacks are occasionally considered serious: the larvæ feed upon the pollen grains and the saccharine cells in the axils of the leaves. Larvæ of *Merodon* and *Eumerus* attack and destroy bulbs of *Narcissus*, *Amaryllis*, etc., and may occur separately or in association. They are well known pests in Europe and have been introduced, along with their host plants, into N. America and other parts. Larvæ of a few species of the family, more particularly those of *Eristalis*, have been found as accidental parasites in the human body causing myiasis of the intestine.

Section B. SCHIZOPHORA

The Schizophora are divided into the two undermentioned superfamilies.

I.—ACALYPTERÆ (HOLOMETOPA).—Squamæ small or vestigial, usually not concealing the halteres. Small or very small flies, the males not holoptic. Thorax without a distinct transverse suture: cell R_5 almost always widely open.

II.—CALYPTERÆ (SCHIZOMETOPA).—Squamæ well developed, usually concealing the halteres. Moderate sized flies, the males often holoptic. Thorax with a distinct transverse suture: cell R_5 open or closed.

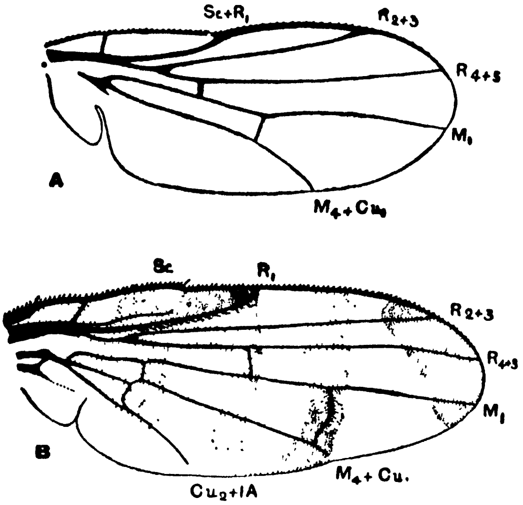

FIG. 613.—VENATION OF ACALYPTERÆ. A, *Chlorops tæniopus*; B, *Trypeta tussilaginis*.

Superfamily I. ACALYPTERÆ

The following table (partly after Williston), although admittedly imperfect, is drawn up as an aid to the recognition of typical members of the group, but it must be pointed out that many of the characters are slight and often ill-defined.

1.	Hymenopterous-like flies with long proboscis, jointed near the middle: ovipositor elongate.	CONOPIDÆ (p. 668)
2.	Eyes on lateral stalk-like prolongations of the head.	DIOPSIDÆ (p. 672)
3.	Beetle-like flies: scutellum very large, covering wings and abdomen.	CELYPHIDÆ (p. 672)
4.	Small dark littoral flies with thorax and abdomen flattened: head bristly.	PHYCODROMIDÆ (p. 672)
5.	Not as above (1–4).	
6 (25).—	Sc distinct, R_1 usually terminating near middle of costa.	
7 (12).—	Vibrissæ present.	
8.	Costa spiny, tibiæ with spurs and preapical bristles.	HELOMYZIDÆ (p. 672)
9.	Small, shiny flies, usually black, with basally constricted abdomen, wings often with a stigma-like spot.	SEPSIDÆ (p. 672)
10.	Somewhat elongate flies with long wings; cross-veins often approximated, R_1 terminating near Sc.	HETERONEURIDÆ (p. 672)
11.	Rather large flies: Sc and R_1 well separated.	CORDYLURIDÆ (p. 672)
12 (7).—	Vibrissæ absent.	
13 (14).—	Femora thickened, hind tibiæ often dilated, scutellum large.	RHOPALOMERIDÆ (p. 672)
14 (13).—	Not such flies.	
15 (18).—	Legs long and slender: cell R_5 narrowed or closed.	

16 (17).—Eyes very large, tarsi longer than tibiæ. TANYPEZIDÆ (p. 672)

17 (16).—Eyes small, tarsi shorter than tibiæ. MICROPEZIDÆ (p. 672)

18 (15).—Legs not noticeably long and slender: wings often marbled or clouded: cell R_5 widely open.

19 (22).—Ovipositor horny: no preapical bristle.

20 (21).—Cubital cell often pointed: upper fronto-orbital bristles only present. ORTALIDÆ (p. 669)

21 (20).—Cubital cell rounded distally: a single fronto-orbital bristle. SAPROMYZIDÆ (Lonchæinæ) (p. 670)

22 (19).—Ovipositor not horny: preapical bristle present.

23 (24).—Two fronto-orbital bristles: 2nd antennal joint not elongated. SAPROMYZIDÆ (Sapromyzinæ) (p. 669)

24 (23).—Fronto-orbital bristles present or absent; 2nd antennal joint often long. SCIOMYZIDÆ (p. 672)

25 (6).—Sc absent or incomplete, R_1 terminating before middle of wing.

26 (27).—Hind metatarsi dilated and shortened. BORBORIDÆ (p. 672)

27 (26).—Hind metatarsi not dilated and always longer than succeeding joint.

28 (33).—Cells M and 1st M_2 usually confluent.

29 (32).—Vibrissæ rarely distinct.

30 (31).—No lower fronto-orbital bristles: arista usually bare. OSCINIDÆ (p. 671)

31 (30).—Lower fronto-orbital bristles present: arista rarely bare. EPHYDRIDÆ (p. 671)

32 (29).—Vibrissæ distinct: arista plumose, eyes usually red. DROSOPHILIDÆ (p. 670)

33 (28).—Cells M and 1st M_2 separate.

34 (37).—Vibrissæ usually present.

35 (36).—Upper fronto-orbital bristles only present, no mesopleural or prothoracic bristles: arista bare. PIOPHILIDÆ (p. 672)

36 (35).—Lower fronto-orbital bristles present, and convergent, mesopleural and one prothoracic bristle also present: arista usually pubescent. AGROMYZIDÆ (p. 670) and GEOMYZIDÆ (p. 672)

37 (34).—Vibrissæ absent.

38 (39).—Wings conspicuously marbled, Sc sharply curved upwards. TRYPANEIDÆ (p. 669)

39 (38).—Wings not conspicuously marbled, Sc absent or indistinct. PSILIDÆ (p. 672)

FAM. CONOPIDÆ.—HEAD LARGE, BROADER THAN THORAX: ANTENNÆ PORRECT RATHER LONG, 3RD JOINT CLUBBED WITH AN APICAL STYLE OR DORSAL ARISTA. PROBOSCIS USUALLY LONG AND SLENDER, FOLDING NEAR ITS MIDDLE. CUBITAL CELL VERY LONG. GENITALIA CONSPICUOUS AND CURVED BENEATH THE BODY.

A family of more or less elongate, moderate-sized flies, thinly pilose or almost bare, and frequently bearing a striking resemblance to solitary wasps or other Hymenoptera. Most species visit flowers; they are slow fliers and less than 20 kinds occur in the British Isles. The larvæ are endoparasites of adult bees and wasps or of Orthoptera (vide de Meijere, 1903, 1912). The species of *Conops* parasitize *Bombus, Odynerus, Sphex, Vespa,* etc.: *Psilocephala* parasitizes *Apis, Xylocopa,* and *Bombus,* while *Myopa* is known to attack *Andrena, Bombus* and *Vespa* (vide Seguy, 1928).

The eggs of the Conopidæ are elongate oval with a group of hooks, filaments, or other outgrowths at the micropylar end. In certain cases the eggs are stated to be deposited on the bodies of the hosts during flight. The larvæ are generally found in the region of the anterior abdominal segments of the host, and are attached by their hinder extremity to a large trachea or air-sac: the exact relation between the Conopid larva and the tracheal system of the host is in need of further investigation. The mouth-parts are greatly reduced and the larvæ are mainly hæmophagous. In general shape the larvæ are ovoid or pyriform with considerable powers of changing their form. Their most conspicuous features are the large convex plates of the posterior spiracles. The latter are complex structures, and distributed over the surface of each spiracle is a series of small sieve-like areas.

FAM. ORTALIDÆ.—FRONT BROAD IN BOTH SEXES: LOWER FRONTO-ORBITAL BRISTLES AND VIBRISSÆ ABSENT. WINGS ALMOST INVARIABLY MARBLED, SC AND R_1 ENTIRELY SEPARATED THOUGH OFTEN CLOSELY APPROXIMATED. MIDDLE TIBIÆ ALONE SPURRED, NO PREAPICAL BRISTLE. OVIPOSITOR CORNEOUS, 3-JOINTED.

A large family many of whose members have mottled wings and consequently resemble Trypaneidæ. Unlike the latter family, Sc meets the costa at an acute angle and is not abruptly elbowed distally. In the male there are 5 evident abdominal segments and an elongate rolled up ædeagus: in the female there are 6 abdominal segments with a flattened corneous ovipositor. The flies are commonly met with wherever there is abundant vegetation, and rather more than 2 dozen species are British. According to Banks (1912) the larvæ are usually more slender than those of the Muscidæ; the anterior spiracles have about 10 lobes and the posterior pair are borne on two slight processes, each spiracle being provided with three short slits. The larva of *Platysoma umbrarum* is described by Perris (1855) and that of *Euxesta nitidiventris* Lw. by Brues (1902). The latter species lives beneath the bark of dead trees and is 11-segmented with the head nearly as long as the first two thoracic segments. The larva of *E. notata* Wied. attacks oranges, apples, onions, cotton bolls, etc., and has also been found in human excrement.

FAM. TRYPANEIDÆ (Trypetidæ).—FRONT BROAD IN BOTH SEXES, LOWER FRONTO-ORBITAL BRISTLES PRESENT, VIBRISSÆ WANTING. WINGS MOTTLED WITH A BROWN OR YELLOWISH PATTERN: SC SHARPLY BENT DISTALLY TOWARDS COSTA, BECOMING INDISTINCT NEAR THE APEX. MIDDLE TIBIÆ SPURRED, NO PREAPICAL BRISTLE: OVIPOSITOR PROMINENT, CORNEOUS, 3-JOINTED.

The Trypaneidæ or "fruit flies" form an easily recognizable and natural family of almost cosmopolitan distribution. According to Bezzi 875 species were known up to 1913, of which 64 are British: the wings as a rule are conspicuously marbled and the venation (Fig. 613) is the most complete among Acalypteræ (Loew). The horny, flattened ovipositor is very characteristic and in *Toxotrypana* it exceeds the total length of the insect. It is noteworthy that a corneous ovipositor is also found in *Lonchæa* and the Ortalidæ but, in the latter, the lower fronto-orbital bristles are wanting, and Sc is distinct throughout. The standard systematic work on the family is that of Loew (1862): the important papers of Bezzi (1913) and Enderlein (1911) should also be consulted. The larvæ are phytophagous and those of several species are well known. When fully grown they are rounded or barrel-shaped: a pair of rounded anal tubercles are present, and the posterior spiracles each contain three simple slits. The prothoracic pair are many-lobed, from about 14 to 38 processes being present.

Trypaneid larvæ may be grouped under four headings with reference to their habits. (1) Living in fruits, preferably of the fleshy type: *Dacus, Ceratitis,* etc. (2) Living in the flower heads of Compositæ: *Trypanea, Urophora,* etc. (3) Leaf-miners, or living in stems or buds: *Acidia, Spilographa,* etc. (4) Gall formers on various parts of plants.

Ceratitis capitata Wied. is the well known Mediterranean fruit fly (Quaintance, 1912) whose larva attacks almost all commercial and other succulent fruits, and becomes extremely injurious wherever established. The eggs are deposited inside the fruit, and the whole life-cycle occupies about 30 to 40 days, pupation taking place in the ground. This species occurs throughout the tropics and warmer regions, including the Mediterranean countries of Europe. *Acidia heraclei* L. (vide Smith and Gardner, 1922) is the celery fly whose larvæ cause considerable damage by mining the leaves of that plant and the parsnip: it also affects certain wild Umbelliferæ. The life-history of *Urophora solstitialis* is described by Wadsworth (*Ann. App. Biol.*, 1914) and that of *Dacus cucurbitæ* by Back and Pemberton (*U.S. Bull.*, 471). Observations on the anatomy of the larva and imago of *Dacus tsuneonis* are given by Miyake (1919).

FAM. SAPROMYZIDÆ.—FRONT WITH A SINGLE ROW OF BRISTLES ON EITHER SIDE, VIBRISSÆ WANTING: 3RD ANTENNAL JOINT MORE OR LESS ELONGATE. SC DISTINCT THOUGH OFTEN APPROXIMATED TO R_1. TIBIÆ USUALLY WITH PREAPICAL BRISTLE, MIDDLE PAIR SPURRED. OVIPOSITOR PROMINENT, USUALLY NOT HORNY.

A family of small flies often with marbled wings. Williston includes in the group the Lonchæidæ of Loew and others, which are frequently regarded as a separate family. The larvæ of *Sapromyza* are scavengers, and possess a dorsal transverse row of conical tubercles on the penultimate segment which is absent in *Lonchæa.* The larva of the latter genus has been fully described by Cameron (*Trans. Ent. Soc.*, 1913) and Silvestri (1917A): that of *L. chorea* has been found in cow-dung, rotting vegetation and diseased bulbs and roots. In *L. aristella* the larval existence is passed in the flowers and fruit of the olive in Italy. The body is narrow and cylindrical, tapering somewhat anteriorly: the prothoracic spiracles are 9-lobed, and the posterior pair is provided with three slits placed at right angles to one another. In *Lauxania ænea* Fall. the larva mines the leaves of clover (Marchal, *Bull. Soc. Ent. Fr.*, 1897).

FAM. AGROMYZIDÆ.—FRONT BRISTLY OR OTHERWISE, VIBRISSÆ USUALLY PRESENT. ARISTA BARE OR PUBESCENT, NOT DEFINITELY PLUMOSE. WINGS RATHER BROAD, SC VESTIGIAL OR ONLY SEPARATE BASALLY FROM R_1; CELLS M AND CU ALWAYS SMALL, FORMER SOMETIMES CONFLUENT WITH IST M_2.

A family of small to minute flies, of ill-defined limits which graduate through certain genera into the Geomyzidæ. The life-histories have been followed in a number of cases and the larvæ are usually leaf-miners. Their range of food plants varies greatly; thus *Phytomyza chrysanthemi* is apparently confined to the Compositæ while *Agromyza pusilla* Mg. utilizes species belonging to many natural orders. *A. æneiventris* Fall. is stated to tunnel into the roots and leaves of clover, while *A. pruinosa* Coq. mines the cambium of birch and hazel. Larvæ of *Leucopis* have the unusual habit of preying upon aphids and coccids. The majority of species of the family pass through several generations in the year—five or more in the case of *Agromyza pusilla.* The larvæ are cylindrical, tapering somewhat anteriorly, and more or less truncated posteriorly. The mouth-parts are conspicuous on account of their dark colour and strong chitinization: on the ventral surface of the anal segment is a small sucker-like organ. The posterior spiracles are situated at the apices of backwardly projecting processes of variable length, usually contiguous and porrect. The puparia are broadly fusiform with the segments well defined: both the anterior and posterior spiracles are prominent and projecting. Pupation either occurs in the larval mine or in the soil. For information on the metamorphoses of various species reference should be made to the papers of Perris (1870) for *Leucopis*; Phillips (*Journ. Agric. Res.*, 1914) for *Agromyza parvicornis*; Malloch (1915A) for *A. pruni*; Webster and Parks (*Journ. Agric. Res.*, 1913) for *A. pusilla*; Miall and Taylor (1907) and Smulyan (*Mass. Exp. Sta. Bull.* 157, 1914) for *Phytomyza*; and Barnes (*Ann. Appl. Biol.* 1933) for the cambium miner *Dizygomyza.* The most remarkable life-cycle occurs in *Cryptochætum,* whose larvæ are endoparasites of Coccidæ. In *C. iceryæ,* which parasitizes *Icerya,* there are four larval instars (vide Thorpe, 1931). The 1st instar larva is an embryo-like sac devoid of tracheæ and mouth-parts, with the digestive canal closed: caudally it bears a pair of finger-like processes. In the successive instars the caudal processes increase in length and become filamentous until, in the last stage, they are much longer than the whole body: these organs appear to be mainly respiratory in function. A characteristic feature of the larvæ of this family is the presence of sphæroidal concretions of calcium carbonate in the Malpighian tubes and these products appear to be only wanting in *Cryptochætum* and *Leucopis* which are carnivorous in habit.

FAM. DROSOPHILIDÆ.—FRONT WITH CONSPICUOUS BRISTLES, 3RD ANTENNAL JOINT ROUNDED OR OVAL, ARISTA PLUMOSE OR PECTINATE: VIBRISSÆ EVIDENT, EYES USUALLY RED; SC VESTIGIAL, R_1 VERY SHORT AND THE COSTA INCISED NEAR ITS TERMINATION; CELLS M AND IST M_2 USUALLY CONFLUENT.

The flies pertaining to this family usually have a somewhat swollen appearance, with light red eyes, and are commonly taken by sweeping herbage. Others are prevalent about decaying fruit, cider presses, wine vats, vinegar factories, etc., where they are attracted by certain by-products of fermentation. The eggs of *Drosophila* are often spindle-shaped, bearing elongate processes at one extremity: as the eggs are frequently submerged in fluid media, with the filaments at the surface, it has been suggested that the latter are concerned with respiration. The larva is 11-segmented with each segment surrounded by a girdle of minute hook-like spines (*D. funebris*), or the body may be uniformly invested with these structures (*D. fenestrarum*). Three pairs of conical lateral outgrowths are borne on the anal segment, together with a longer median retractile process, carrying the posterior spiracles. In addition to occurring in fermenting fruit (*D. melanogaster*), in vinegar vats (*D. funebris*) or in excrement, other larvæ mine the leaves of various plants. The pupæ are fusiform with the anterior dorsal surface flattened to form an ovoid plate which is forced upwards to allow of the eclosion of the imago. Arising from this plate is a pair of stalked, digitate or plumose spiracular processes. Traces of the anal processes of the larva are also evident upon the puparium. For an account of the life-history of *D. funebris* vide Unwin (1907).

FAM. EPHYDRIDÆ.—ARISTA PLUMOSE, OR PECTINATE DORSALLY, RARELY BARE ; ORAL CAVITY USUALLY VERY LARGE, VIBRISSÆ INDISTINCT. SC FOR THE MOST PART CONFLUENT WITH R_1, SEPARATE ONLY BASALLY ; COSTA INTERRUPTED NEAR POINT OF JUNCTION WITH THIS VEIN. CELL M CONFLUENT WITH 1ST M_2, CELL CU USUALLY VESTIGIAL. MIDDLE TIBIÆ SPURRED, NO PREAPICAL BRISTLE.

The flies of this family are black or darkly coloured, inhabiting marshy places, damp meadows, etc. The family is closely related to the Drosophilidæ and clear distinctions are sometimes difficult to recognize. Jones (1916) has described the life-history of *Ephydra millbræ* which is aquatic. The eggs are partially clothed with hairs and are attached to floating vegetation, etc. The amphipneustic larvæ are densely covered with short pubescence, with the anterior spiracles 7-branched, and a pair of respiratory tubes emerge from a terminal anal siphon. Eight pairs of conspicuous pseudopods, armed with hooks, are present on the abdomen. The puparium is provided with an elongate siphon whose apex rests at the surface of the water. Larvæ of *Notiphila* occur in the stems of water plants, while those of *Hydrellia modesta* L. are found in the leaves of *Potamogeton* and are metapneustic throughout life (Keilin, 1915). Other larvæ occur in salt or alkaline waters, particularly those of *Ephydra hians* Say and *E. californica* Pack. which often appear in such vast numbers as to have been used by the N. American and Mexican Indians as food. An account of the anatomy of the larva of *E. riparia* is given by Trägårdh (1903) and the metamorphosis of *Teichomyza fusca* by Vogler (*Ill. Zeits. Ent.*, 1900). The larva of *Psilopa petrolei* (Thorpe, 1930) is a veritable biological curiosity since it has long been known to live in pools of crude petroleum in California. Morphologically it differs little from many other Ephydrids and its adaptation to its mode of life appears to be physiological. The food of this larva consists of insects trapped in the oil and possibly of bacteria which occur in that medium.

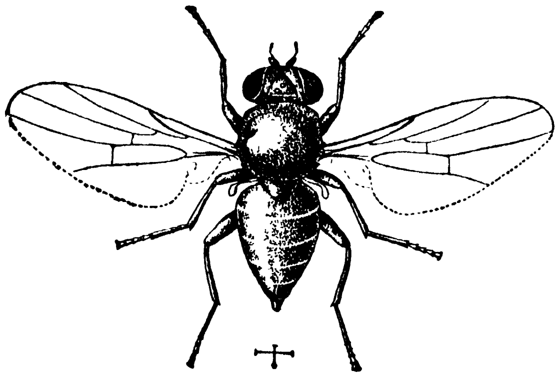

FIG. 614.—*Oscinella frit*.

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FAM. OSCINIDÆ (Chloropidæ).—ARISTA USUALLY BARE, ORAL CAVITY SMALL, VIBRISSÆ RARELY PRESENT. SC VESTIGIAL OR WANTING, CELLS M AND 1ST M_2 CONFLUENT, CELL CU VESTIGIAL OR ABSENT (Fig. 613). TIBIÆ WITHOUT PREAPICAL BRISTLE.

Small, bare, often light-coloured flies, plentiful among miscellaneous herbage about roadsides, meadows, etc. Although closely allied to the Ephydridæ they may usually be separated therefrom by the absence of lower fronto-orbital bristles, the small oral cavity, and the bare arista. The larvæ are essentially phytophagous, although those of a few species are predaceous. The larva of *Oscinella frit* (Steel, 1931) is very narrow in proportion to its length. The anterior spiracles are 6-lobed, and the posterior pair open at the apices of short tubular projections at the hind extremity of the body : each spiracle has three circular openings separated by chitinous ridges. In *Oscinosoma* the larva is less elongate and more musciform with ambulatory swellings on the abdominal segments : the spiracles closely resemble those of *Oscinis* (vide Silvestri, 1917). The larva of *Chloropisca glabra* is predaceous on aphides and its life-history has been followed by Parker (*Journ. Econ. Ent.*, 1918), and the anatomy of the larva of *Platycephala* by Wandolleck (1899). The " frit-fly " *Oscinella frit* (Fig. 614) is a pest of cereals in Europe. The flies of the first generation oviposit in May on the leaves or stems of spring oats and various grasses. The larvæ migrate to the shoots causing the death of the central leaves. Flies of the second generation oviposit during July on the ears of oats, and the larvæ feed on the spikelets and young grain. Oviposition in the third generation occurs during September on winter cereals and various grasses. Winter is passed in the larval condition at the bases of the shoots which they ultimately destroy. The " gout fly " *Chlorops tæniopus* lays its eggs during June on the leaves of spring barley or occasionally on couch grass. The larvæ migrate into the shoots which become thickened and the leaves are distorted. If the barley ear is about to be formed the larva eats a groove down one side of it and the internode. The ear fails to grow away from the ensheathing leaf. The flies of the second generation oviposit from the middle of August until the middle of October mainly on couch grass, but sometimes on self-sown or winter cereals. The shoots become greatly thickened, the leaves distorted, and no ear is formed (Frew, *Proc. Zool. Soc.* 1923 : *Ann. Appl. Biol.* 1924). Certain species of *Siphunculina* and *Hippelates* probably transmit conjunctivitis and other eye diseases in the Orient, California, etc. Such flies have spinous pseudotracheæ which appear to make incisions in the conjunctiva and so aid the entry of pathogenic organisms carried on their bodies (Graham Smith, 1930A).

FAM. CORDYLURIDÆ (Scatomyzidæ).—FRONT BRISTLY AND WELL DIFFERENTIATED FROM ORBITS, VIBRISSÆ PRESENT. WINGS RATHER LARGE, SC CLEARLY SEPARATED FROM R_1. TIBIÆ SPURRED, ABDOMEN WITH AT LEAST 5 EVIDENT SEGMENTS.

These flies are never very small, and are usually considerably larger than most Acalypteræ. They frequent meadows and moist places and many, particularly *Scatophaga*, are found about dung in which the larval life is spent. A few species have been bred from insect larvæ. Cotterell (*Proc. Zool. Soc.*, 1920) has described the life-history of *Scatophaga stercoraria*, and the adults of this genus may often be observed to prey upon other Diptera, but their predaceous habits have been very little investigated. Certain members of the family closely resemble the Anthomyidæ but may be distinguished by the eyes being wide apart in both sexes and by the absence of squamæ. The life-history of *Hydromyza confluens* has been described by Welch (*Ann. Ent. Soc. Am.* 7, 1914), this species being aquatic in the larval instars.

In addition to the foregoing there are a number of families of minor importance which need a brief reference. The MICROPEZIDÆ are a small family represented in Britain by about a dozen species : their members bear a resemblance to the smaller Tipulidæ on account of their long slender bodies and legs. The TANYPEZIDÆ are mostly comprised in the genus *Tanypeza* and are sometimes classified with the preceding family but are clearly distinct : they do not occur in Britain. The SEPSIDÆ are not unlike the Micropezidæ but have rudimentary palpi : rather fewer than 30 species are British. The PIOPHILIDÆ are closely related to the Sepsidæ. *Piophila casei* is the best known member and its larva lives in ham, bacon, cheese, etc. Its biology has been described by Banks (1912) and by Herrick. On account of their peculiar habits of leaping the larvæ are known as " cheese skippers " : the leap is performed by the larva seizing the edge of the anal extremity with its mouth-hooks and suddenly releasing it when in a state of tension. The PSILIDÆ include the well known carrot fly *Psila rosæ* whose larvæ cause much damage by eating into the tap root of the carrot (vide Smith and Gardner, 1922). The RHOPALOMERIDÆ inhabit Central and South America and the GEOMYZIDÆ are a small ill-defined family often difficult to separate from the Agromyzidæ : their larvæ have been found in the stems of plants. The CELYPHIDÆ and DIOPSIDÆ are small tropical families of very aberrant structure and easily recognized by the characters given in the key on p. 667. The PHYCODROMIDÆ mainly inhabit the seashore among weed cast up by the tide : they are typically represented by the common littoral fly *Fucomyia frigida*. The BORBORIDÆ are small black or brownish flies often abundant near decomposing organic matter : several are apterous and *Anatalanta* from Kerguelen I. lacks the halteres also. The HETERONEURIDÆ are not often met with but occur among herbage near streams, etc. : the larva of *Heteroneura albimana* Mg. is described by Perris from rotting wood. The HELOMYZIDÆ are usually recognizable by the bristly costal margin to the wings. Their larvæ have been found in carrion, dung and fungi : for the metamorphosis of *Helomyza livens* vide Gercke (*Verh. Ver. Hamb.*, 1884, 4). The SCIOMYZIDÆ frequent damp situations, their larvæ being aquatic or sub-aquatic. The metamorphoses of *Sepedon* and *Tetanocera* are described by Needham (1901). Both adults and larvæ of *Actora æstuum* frequent the sea-shore and are often subjected to immersion in salt water. According to Joseph (*Zool. Anz.*, 1880) the adults are protected by a waxy exudation which is constantly renewed.

Superfamily II. Calypteræ

Key to the families:

1 (2).—Mouth-parts vestigial: no sternopleural setæ. ŒSTRIDÆ (p. 678)

2 (1).—Mouth-parts well developed: sternopleural setæ present.

3 (4).—Hypopleural setæ present : usually 2 anterior and 1 posterior sternopleural setæ : M_1 usually definitely bent towards R_{4+5} (Fig. 615 B). TACHINIDÆ (p. 675)

4 (3).—Hypopleural setæ absent : usually 1 anterior and 2 posterior sternopleural setæ : M_1 either more or less parallel to R_{4+5} or curved, rather than definitely bent, towards this vein (Fig. 615 A). ANTHOMYIDÆ (p. 673)

FAM. ANTHOMYIDÆ.—This extensive family includes the Muscidæ (excepting *Calliphora* and its allies), together with the Anthomyidæ, of the older works. Its species are small to rather large flies, many of which bear a general resemblance to the house-fly. Although the family includes the hæmophagous genera *Stomoxys, Glossina, Lyperosia* and *Hæmatobia,* in which both sexes suck the blood of man and other mammals by means of piercing mouth-parts, the vast majority of its members are innocuous in this respect. The larvæ (Fig. 575) show great diversity of habit : some are plant-feeders and are serious pests of agriculture and very many inhabit decaying organic matter, more especially of vegetable origin. Of these latter the majority are saprophagous, while the rest are carnivorous preying upon other dipterous larvæ, small Oligochæta, etc., which inhabit the same medium.

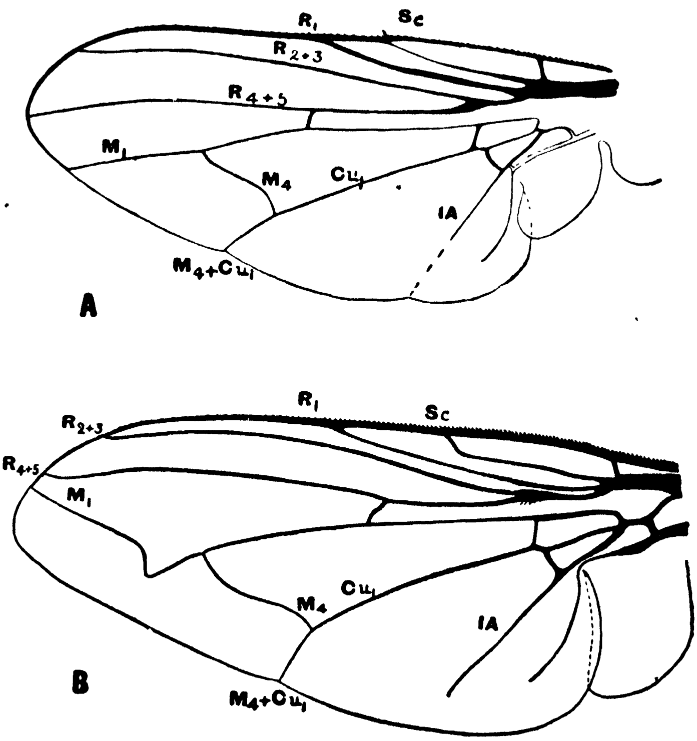

FIG. 615.—VENATION OF A, *HYLEMYIA STRIGOSA* AND B, *CALLIPHORA ERYTHROCEPHALA.*

Musca domestica L. may be taken as a typical representative of the family. It is, as a rule, most abundant during the hottest months of the year and in Europe and N. America attains its greatest numbers from July to September. According to Roubaud, the insect usually does not hibernate but continues reproduction during winter in warm rooms and stables, but further research is much needed with particular reference to various climatic conditions. The eggs are cylindrical-oval, 1 mm. long, with two curved rib-like thickenings along the dorsal side : they are laid in masses of 100–150 and the usual number deposited by a single fly in a life of about 2½ months is probably 600–1,000.[1] The chief breeding places are accumulations of horse manure or stable refuse, but human and other excrement is often selected, and also most kinds of fermenting animal and vegetable substances, particularly the contents of ash bins, etc. At a temperature of 25° C.–35° C. the larvæ hatch in 8–12 hours. The first instar larva is 2 mm. long, metapneustic, and each posterior spiracle opens by a pair of small, oblique, slit-like apertures. This stadium lasts 24–36 hours under favourable conditions. The second instar larva is amphipneustic with larger posterior spiracles and, at a temperature of 25° C.–35° C., the stadium lasts about 24 hours. The third instar is also amphipneustic and measures about 12 mm. long when fully grown. The anterior spiracles have 6–8 processes, and each posterior spiracle is a D-shaped ring surrounding three sinuous slits. Incubated at 35° C. this stadium lasts 3–4 days, and the pupal stadium averages 4–5 days. The developmental cycle, from the egg to the eclosion of the imago, varies in different parts of the world with the temperature and other factors. According to Herms it varies from an average of 44·8 days at 16° C., to an average of 10·4 days at 30° C. Roubaud states that, in a heap of actively fermenting manure in warm weather, the life-cycle may only require six days. The house-fly has an important bearing upon the welfare of man as a carrier of the germs of summer diarrhœa, typhoid and possibly other diseases: there is also evidence pointing to the probability of its acting as a carrier of the eggs of certain species of intestinal worms. Preventive and remedial measures are numerous, and of these the most important is the elimination of the larval breeding places, or the rendering of the latter fly-proof or unsuitable for the insect. The destruction of adult flies must also form part of any system of eradication: this may be brought about by the use of fly traps baited with attractive chemotropic substances, by means of adhesive fly-papers, or by poison baits such as formaldehyde. The literature on this species has assumed extensive proportions: a general account of the insect and its relation to man is given by Hewitt (1914). Observations on its breeding habits are given by Newstead (1907) and Roubaud (*Ann. Inst. Pasteur*, 1922), while the relation of the insect to medical science and sanitation is dealt with by Graham-Smith (1914). Additional observations on this insect and other common flies will be found in papers by the latter author (1916 and 1919).

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[1] Dunn (*Bull. Ent. Res.* 13) states that in Panama a single female may deposit 2,387 eggs during 31 days after emergence.

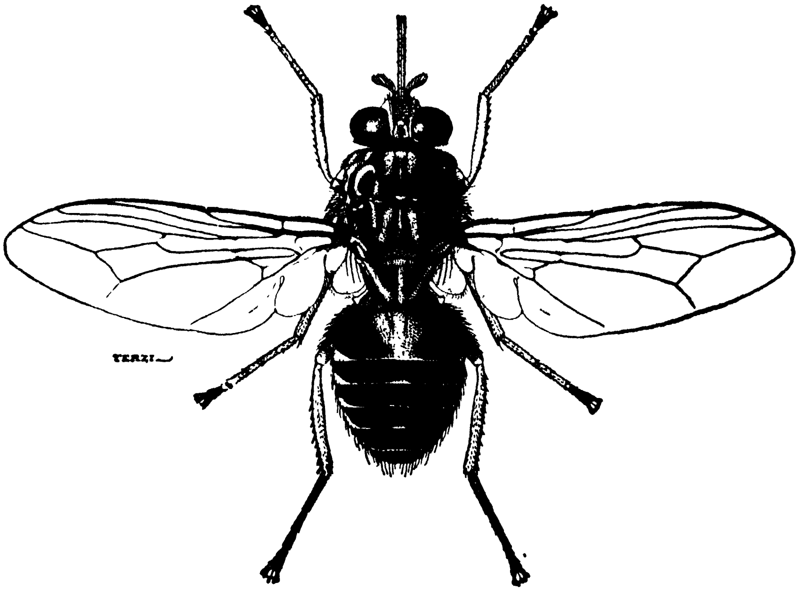

FIG. 616.—*GLOSSINA PALPALIS*, FEMALE. × 5.
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The biting house-fly *Stomoxys calcitrans* breeds principally in horse manure and stable refuse, but the larva may also be found in grass mowings, sewage beds, etc. The life-history has been studied by Newstead (1906), Bishopp (1913), Mitzmain (1913), and others. The duration of the life-cycle depends upon temperature, humidity and the nature of the food supply, while the minimum period for complete development is 23–32 days. According to Newstead two important conditions are necessary for development—an absence of light and an abundance of moisture. The ova are laid in batches of 60–70 and about 600 is the greatest number deposited by one female (during 65 days). At an average day temperature of 72° F., and 65° F. by night, the larvæ hatch out in 2–3 days. When fully grown they measure 11–12 mm. long, and differ from the larvæ of the house-fly in that the hind spiracles are rounded and smaller, with the three apertures on each plate only slightly curved instead of being sinuous. In England, during August, the larval period lasts 2 to 3 weeks and 9 to 13 days are spent as a pupa: in the tropics the pupal stage may only last 4 days.

The species of *Glossina* or Tsetse flies (vide Austen, 1911; Austen and Hegh, 1922; Roubaud, 1909) are now well known to be the carriers of the pathogenic agents of certain virulent diseases in Africa. Thus *Glossina palpalis* (Fig. 616) transmits *Trypanosoma gambiense*, the causal agent of sleeping sickness, from man to man by means of its piercing mouth-parts. In a similar manner *G. morsitans* transmits

Trypanosoma rhodesiense which is responsible for the more local or Rhodesian form of that disease. *Glossina morsitans* is also the chief carrier of the Trypanosomes which cause the disease known as nagana among domestic animals. Although widely distributed through tropical and sub-tropical Africa, species of *Glossina* do not occur continuously throughout that area, but are largely restricted to patches of forest and bush where there is warmth, damp, and shade, such tracts being known as "fly belts." The larvæ in this genus are nourished within the uterus of the parent and, when mature, are deposited singly and at intervals in a shady situation on the ground. When newly born, the larva is yellowish-white, with a black posterior extremity bearing a pair of polypneustic spiracular lobes. It speedily burrows or otherwise conceals itself and pupates, the imago appearing about a month later.

Among the phytophagous members of the family those of agricultural importance are discussed by Smith (1931). For instance, the larva of *Chortophila brassicæ* is extremely destructive to vegetables of the Brassica tribe and also affects wild Cruciferæ. It destroys the roots of those plants and the eggs are deposited around the stem near the soil-level. *Hylemyia coarctata* is the Wheat Bulb Fly, which is a serious pest in many parts of Europe : it is exceptional in laying its eggs on bare soil and not necessarily in proximity to its host plant. The larva of *Pegomyia* are leaf-miners and those of *P. hyoscyami* are destructive to beet and mangolds. In the case of *Anthomyia spreta* the larva feeds on the fungus *Epichlöe* which attacks grasses, the fly laying a single egg in each patch of mycelium (Trägårdh, *Arkiv. Zool.* 1913).

The carnivorous forms have been studied in detail by Keilin (1917) and are more especially enemies of saprophagous larvæ of other Diptera. They include species of *Melanochelia*, *Graphomyia*, *Phaonia*, *Mydæa*, *Hydrotæa* and other genera. Perhaps the most remarkable of the carnivorous larvæ are those of *Passeromyia* which are blood-sucking parasites of birds (Rodhain and Bequaert, 1916). The larvæ of certain species of *Mydæa* are also subcutaneous avian parasites (Nielson, 1911). Mention needs also to be made of the larvæ of *Fannia* which live in excrementous and other decaying organic matter. They are unusual in being broad and somewhat flattened with paired segmental outgrowths of the body-wall (vide Hewitt, 1912).

For a general account of the family, including keys to the identification of most of the British species, the work of Seguy (1923) should be consulted.

FAM. TACHINIDÆ.—Included in this family is a vast assemblage of mostly bristly flies which are characterized by the presence on the hypopleura of a row of setæ, placed like a screen, in front of the metathoracic spiracle, on either side (Fig. 582 A). Their larvæ are essentially carnivorous and are largely parasites of other insects or less often feed on flesh or decomposing animal remains. Over 140 genera and more than 200 species are British ; for their identification the works of Wainwright (1928, 1932) and of Lundbeck (*Diptera Danica*, vol. 7) should be consulted.

The Sarcophaginæ are characterized by the arista being plumose up to, or slightly beyond, the middle and bare distally : macrochætæ are usually only present on the distal part of the abdomen, the disc being rarely bristly, and the eyes are but little approximated in the male. The sub-family includes comparatively few genera but numerous species, often very much alike. For the most part they are uniformly coloured flies, with a grey longitudinally striped thorax, and marbled abdomen. The larvæ (vide Thompson, 1921) are of the Muscid type and taper anteriorly with the posterior extremity rounded. Transverse bands of denticles differentiate the segments, and the posterior spiracles are situated in a deep stigmal pit bearing, as a rule, three straight subparallel slits. The larvæ occur in decaying animal or vegetable matter or are parasites of insects and other animals (vide Aldrich, 1915). Their hosts include Orthoptera, Lepidopterous larvæ, adult Coleoptera, scorpions, earthworms, etc. ; snails are also not infrequently utilized as hosts. According to Pantel (1910) the parasitic larvæ lie free within the body of their insect hosts, and do not acquire any organic connection with the latter as in Tachinids. Species of *Sarcophaga* (or flesh flies) are larviparous, with large eggs, and the uterus is greatly enlarged to form an incubatory pouch : on an average a female will deposit 40–80 larvæ in their 1st instar. Although mainly living in decaying flesh the habits of this genus are extremely varied. Several species parasitize grasshoppers (Kelly, *Journ. Agric. Res.*, 1914), their larvæ boring beneath the body-wall of the host soon after deposition. Others have been found beneath the skin of tortoises, in the stomachs of frogs, in snails (Keilin, 1919) or causing nasal myiasis in man : *S. hæmatodes*, however, is coprophagous. Fabre observed that the carrion fly *S. carnaria* will deposit its larvæ from a height of 26 inches, and that the ordinary wire meat cover affords imperfect protection, since the larvæ can fall through the mesh unless the latter is very fine *Wohlfartia magnifica* Sch. is abundant in Russia, causing great suffering to domestic animals owing to even the smallest wound becoming infected with its larvæ: in man it often causes myiasis of the ear, nose, eyes, etc. The fly is probably concerned with the spread of foot and mouth disease, but does not occur in Britain. In *Helicobosca muscaria* Mg., a parasite of snails, the larviparous method of reproduction reaches a high degree of specialization: the female produces a single enormous egg which gives rise to a correspondingly large-sized larva (Keilin, 1916). The species of *Miltogramma*, *Metopia* and their allies live, as larvæ, in the nests of solitary bees and wasps which burrow in the ground. The female fly lays the eggs in the nests of the bees, or on the prey of the wasps, and the resulting larvæ devour the food of their hosts.

The Calliphorinæ are very often metallic green or blue flies and are distinguished by the weak development of the macrochætæ, which are usually absent from the dorsal surface of the abdomen: the arista is markedly plumose, usually for nearly its whole length. Many of the species are of importance in medical and veterinary science and in the typical genus *Calliphora*, which includes the well-known " blue bottles " or " blow flies," the larvæ occur in carrion, flesh, etc. *Lucilia* includes the " green bottle flies." The almost cosmopolitan *L. cæsar* breeds in carrion and excrement while *L. sericata*, the " sheep maggot fly," lays its eggs on the wool of sheep: its larvæ bore into the flesh, causing death when present in large numbers. In Australia the sheep blow-fly problem of cutaneous myiasis is one of great importance. The species *Lucilia cuprina* is of primary significance in this connexion and passes its larval development on the living sheep. *L. sericata* and species of *Calliphora* may also play a part in initiating the attack. They are followed by secondary flies, including *Chrysomyia rufifacies*, and other forms, which take advantage of the diseased conditions thus set up. Tertiary flies may also participate during the end-stages of the attack on the sheep. There is thus involved a complex biological association of larvæ which entails great losses among the flocks (vide *Rep. of Joint Blowfly Committee*, 1933). Among other Calliphorinæ producing myiasis is *Aucheromyia luteola*, whose larva is the Congo " floor maggot," frequenting the floors of native huts, and is an ectoparasite sucking human blood (Roubaud, 1913). *Phormia* (*Protocalliphora*) *azurea* is an ectoparasite in the nests of swallows, larks, sparrows and other birds: its larvæ suck the blood of nestlings, attaching themselves to the skin by means of a sectional disc on the 1st segment (vide Coutant, 1915; Roubaud, 1907). The larvæ of *Chrysomyia macellaria*, the " screw-worm fly " of N. and S. America, and of *Cordylobia anthropophaga*, the " tumbu fly " of Africa, cause cutaneous myiasis in man and other mammals.

Since the Great War the saprophagous propensities of certain Calliphorines have been put to practical advantage by the late W. S. Baer, of Baltimore, and others in dealing with chronic osteomyelitis in man. When reared under sterile conditions larvæ of *Phormia regina* and of *Lucilia*, introduced into wounds, were found to clear away suppurating tissues, and inhibit bacterial growth, better than other methods of treatment.

The " cluster fly " *Pollenia rudis* is a parasite of earthworms of the genus *Allolobophora* (Keilin, 1915). The eggs are laid in the earth in September, and the young larva probably makes its way through the genital aperture into the vesicula seminalis of its host, where it remains during the winter. At the beginning of May it awakens and enters the body-cavity, if it has not already done so earlier. For a period of 1 to 4 days it migrates forwards and, during the last part of the journey, its spiracular extremity is directed towards the prostomium of the worm. Arriving at the latter region, it wears through the body-wall by means of the denticles around the anal segment, and the spiracles are thus placed in communication with the exterior. Six to ten days after perforating the prostomium the larva moults and, growing considerably, eats its way into the pharynx of the worm. After a further period of 9 days it passes into the 3rd instar, and gradually eats its way backwards until only the hinder segments of the host remain: pupation subsequently takes place, and the imago appears in 35 to 45 days. A very similar host relationship occurs in the genus *Onesia* (vide Fuller, 1933).

The third group, or the Tachininæ, forms by far the largest division of the family. As larvæ its members are uniformly parasites of other insects, or rarely of other arthropods. They are conspicuously bristly flies, thinly or not at all pilose and with the abdomen clothed with marginal, lateral and discal setæ: the arista is most often bare (Fig. 617). Their habits are very much alike and they are mostly found among vegetation, particularly on flowers. Biologically they are of great interest and importance and Pantel (1910) has divided the species into a number of groups according to their manner of placing the eggs. Briefly, it may be said that many species have ovoid eggs, flattened below, and cement them to the skin of the host; the resulting larvæ speedily bore their way internally (*Gymnosoma, Thrixion, Winthemia, Tachina,* etc.). Others are virtually viviparous since the larvæ hatch immediately and are deposited on the bodies of the future hosts (*Exorista, Voria, Plagia,* etc.). Numerous species lay abundant small darkly coloured eggs on plants: these eggs are swallowed with the food and hatch within the bodies of the hosts (*Sturmia, Rhacodineura, Xenillia, Gonia,* etc.). A considerable number of Tachinines lay their eggs in situations frequented by the hosts: these hatch almost immediately into migratory and often armoured larvæ which bore their way into the first suitable host (*Digonochæta, Echinomyia, Dexia, Prosena,* etc.). There are again others which pierce the host with a special spine-like apparatus and deposit their eggs, or larvæ, internally (*Ocyptera, Allophora, Compsilura*).

Tachinines select as their hosts larval and adult Coleoptera, Orthoptera and Hemiptera, but most often parasitize lepidopterous larvæ and to a lesser degree those of Hymenoptera: in a few instances they are known to select larval Diptera, land Isopods or Myriapods. Their larvæ are usually broadly cylindrical, tapering but little towards the anterior extremity, and with rather indistinct segmentation. The anterior spiracles are small but the posterior pair is conspicuous and often darkly coloured owing to sclerotization. Most of what is known of the biology of the sub-family is due to the researches of Pantel (1898–1910), Nielsen (1909), Thompson (1923 onwards) and Baer (1920).

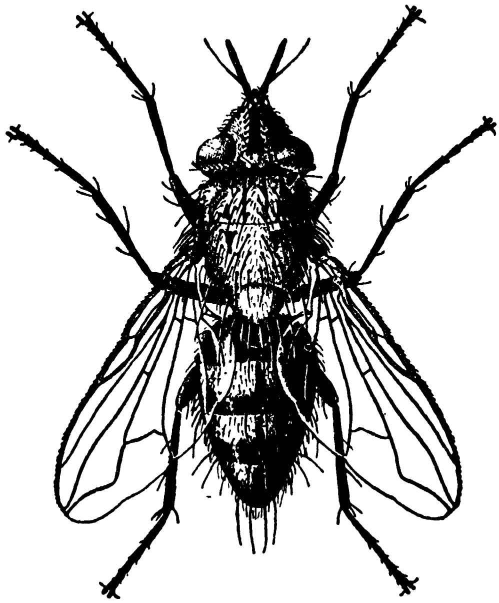

FIG. 617.—*CENTETER CINEREA*, FEMALE.
From *Bull.* 1429 *U.S. Dept. of Agric.*

Within their hosts the larval life of Tachinines presents many variations but, in some stage of existence, they respire free air either by means of a perforation in the body-wall of their host, or by means of a secondary connexion with the tracheal system of the latter. In either case, the larva is enclosed in a sheath ("gaine de fixation" of Pantel, funnel or siphon of other observers) which may be either primary or secondary.

(1) The PRIMARY SHEATH: this is always cutaneous in origin, and is formed as an ingrowth from the lips of the original perforation by means of which the larva enters the host. This perforation persists as an air-hole ("soupirail" of Pantel) and the larva hangs, head downwards, with its spiracles respiring free air through the aperture. The sheath consists of an inner layer of chitin and an outer layer of hypodermis; it grows around and closely embraces the parasite and maintains the latter in position. The sheath may be complicated by the adherence of the degenerating surrounding tissues which are often soldered together by the profuse secretion of chitin by the hypodermis. In this manner muscle fibres, fat-body and tracheæ, along with dead phagocytes may become involved, the whole forming a dense, compact sheath surrounding the parasite. This type of sheath occurs in *Echinomyia fera, Winthemia 4-pustulata,* etc.

(2) The SECONDARY SHEATH: this may be either cutaneous or tracheal in origin according to the position of the air-hole. In species in which this type of sheath obtains, the parasite lives for a while free in the body-cavity of its host as in *Thrixion* or within some particular organ (nervous system, muscles, etc.) as in *Plagia trepida* and *Sturmia sericariæ* (vide more especially Pantel, 1909; Sasaki, 1886). Sooner or later, owing to the respiratory needs of increasing growth, it seeks communication with the air. By means of the anal extremity the larva gradually bores its way either through the integument, or into a tracheal trunk, and thus forms a secondary air-hole. Whichever situation is chosen, a sheath grows round the larva either by means of an ingrowth of the integument (*Thrixion*) or as an outgrowth from the wall of a trachea or of an air-sac (*Blepharidea, Siphona, Gymnosoma*). In either case the parasite becomes enclosed as in the primary sheath. Whichever way it is formed, the

sheath is a pathological reaction of the host against irritation and microbic infection induced by the presence of the parasite. In *Compsilura* and *Sturmia* the parasite acquires a direct connexion with a spiracle of the host, and the sheath under these circumstances is little more than a collar-like rim around the caudal end of the parasite.

The mode of life of the parasite within its host varies not only among different Tachinines, but also during the life of an individual species. Thus in *Thrixion*, for example, the larva devours only the blood and fat-body and forsakes the host while the latter is alive. Furthermore, it does not void excretory matter until it leaves its host. In similar cases, in which the first diet of the larva consists of the blood plasma of the host, the surrounding sheath is closed, absorption taking place according to Pantel by means of " physiological filtration " : at a later stage the buccal armature pierces the sheath and the larva then commences to devour the fat-body. The greater number of Tachinines rupture the surrounding sheath in the 3rd instar and, becoming free in the body-cavity of the host, they commence to devour the vital organs of the latter. In certain other Tachinines a still more complex mode of life is followed : thus in *Sturmia sericariæ* (Sasaki, 1886), which parasitizes the silkworm, the eggs are deposited on mulberry leaves and are swallowed along with the leaf-tissue by the host. The eggs hatch in the gut of the latter, and the young larvæ bore their way through the wall of the digestive canal, and penetrate into the ganglia of the nervous system. At a later stage they forsake the latter, and acquire connexions with the spiracles of their host. Other species similarly live an intraörganic life within the nervous system, muscles, etc., of the hosts, during part of their existence (Pantel, 1909, 1910). Such species have remarkably small eggs adapted for being swallowed by their host. Pupation in Tachinines takes place as a rule in the soil : in some species, however, such as *Carcellia gnava*, which is a parasite of *Malacosoma neustria*, the pupal stage occurs within the pupa of the host. While the Tachinines are here regarded as a single sub-family, modern taxonomists often separate them, on imaginal characters, into several groups, viz. the Phasiinæ, Tachininæ (*sen. str.*), Rhinophorinæ and Dexiinæ. These groups are not, however, sharply defined and various annectant genera occur.

FAM. ŒSTRIDÆ (Warble or Bot Flies).—A comparatively small family of stoutly built more or less pilose flies, often bee-like in appearance. The antennæ are short and partially sunken in facial grooves and the venation almost always is of the Tachinid type. There are no sternopleural setæ while the hypopleural setæ are represented by a group of hairs. The ovipositor is extensile and often long but not adapted for piercing : the eggs are laid on the body hairs of the hosts and are provided with special clasping flanges. The larvæ are endoparasites of mammals but, with few exceptions, the life-histories are imperfectly known owing to difficulties attending observations of the cycle in the living animal.

While the Œstridæ are usually regarded as a separate family, they have definite affinities with the Tachinidæ with which they are associated by some authorities. The taxonomic position of *Gastrophilus* is problematical : some writers elevate the genus to family rank : Seguy places it as a sub-family of the Anthomyidæ, while other authorities retain it as an anomalous group of the Œstridæ. The venation is of the Anthomyid type and there are no hypopleural hairs or setæ, while the squamæ are much smaller than usual among Calypteræ.

Œstridæ are more frequently met with as larvæ than as adults, and a number of species have been described from the larval phase only : only nine species occur in Britain. Parasitization of the mammalian hosts occurs in three ways : in the stomach and intestines, in the nasal and pharyngeal cavities, and beneath the skin. As a rule each species parasitizes a single species of host, and each genus or group of allied species attacks allied hosts. The larvæ, when fully grown, are broadly cylindrical or somewhat barrel-shaped, narrowing relatively little at the extremities, and never tapering anteriorly in a manner comparable with other cyclorrhaphous larvæ. Twelve segments are present with the first two much reduced and annular. The body-wall is very tough with lateral swellings and groups of spinules. As a rule Œstrid larvæ are metapneustic ; in *Gastrophilus* the anterior spiracles are sieve-like, and apparently functional, and the tracheal system is consequently amphipneustic. Carpenter and Pollard (1918) have detected the presence of 6 pairs of vestigial lateral abdominal spiracles in *Hypoderma* and *Œdemagena*. Mouth-hooks are present in all 1st stage Œstrid larvæ but subsequently they may become reduced or vestigial. *Hypoderma* is unique among Cyclorrhapha in that there are five larval instars.

The larvæ feed upon the serous and other exudations into the tissues of their hosts, which fluids are usually either altered or increased owing to irritation induced by the presence of the parasites. When mature the larvæ leave their hosts and pupate in the ground or among surface litter.

Hypoderma includes the well known "warble flies," *H. bovis* and *H. lineatum*. The adults are active from May to August and the eggs are mostly laid on the hairs of the flanks, legs, and feet of cattle. According to Hadwen *H. lineatum* lays 1–14 eggs on a single hair, usually between the point of the hock and the ischium, and on the inside of the legs. *H. bovis* lays its eggs singly on the hairs, chiefly about the legs. In both species they hatch in 4 to 5 days, and the larvæ bore their way beneath the skin, and migrate for several months through the body, until they reach the wall of the gullet. Here they are found from late summer until winter: from December onwards they commence to arrive beneath the skin of the back. Later, the skin is pierced and the posterior spiracles then communicate with the exterior. From February until May or later the fully grown larvæ are found in the swellings or "warbles" on either side of the spine of the host-animal. Ultimately each larva works its way out and falls to the ground where it pupates. The pupal instar lasts about 5–6 weeks. Squeezing out the larvæ is the best remedy at present available as no efficient preventive methods have been devised. The injuries caused by the perforation of the hide, and the deterioration of the flesh, and reduction in the milk occasioned by the presence of these larvæ, entail great losses to the trades concerned. Further research is needed to ascertain the course followed by the young larvæ during their migration from the skin to the gullet. Not infrequently they are found in the spinal canal having apparently deviated from their normal path after leaving the gullet. Most of what is known of their biology is contained in the papers of Hadwen (1912, 1916) and Carpenter and his co-workers (1908 onwards) and in the bulletin (No. 1369, U.S. Dept. Agric., 1926) by Bishopp, Laake and collaborators.

The sheep nostril fly (*Œstrus ovis*) is usually larviparous depositing its larvæ in the nostrils of sheep. The young larvæ migrate into the frontal sinuses of the head where they attach themselves to the mucous membrane. When mature they release their hold and leave the animal. The presence of these parasites causes nasal discharge in the sheep and often obstruction of the air passages. The human warble-fly (*Dermatobia hominis*) is widely distributed in N. and S. America. The females seize mosquitoes, particularly *Psorophora*, and attach the eggs to these vectors (Sambon, *Journ. Trop. Med. and Hyg.* 25, 1922): more rarely Anthomyidæ are utilized for this purpose. When the mosquito, or other carrying insect, settles on man the warmth evidently induces eclosion of the larvæ which bore their way beneath the skin and cause warble-like swellings. In addition to man most kinds of domestic animals function as hosts.

The horse bot-flies (*Gastrophilus*) also lay their eggs on the hair (vide Dove, 1918; Hadwen and Cameron, 1918). In *G. intestinalis* they are found on various regions, preferably the fore-legs. The young larvæ hatch upon the application of moisture and friction supplied by the licking of the horse: they are ingested, and attach themselves to the walls of the stomach. *G. nasalis* oviposits on the hairs beneath the jaws, and to some extent on the shoulders, etc. The larvæ attach themselves to the pharynx, stomach, and duodenum. *G. hæmorrhoidalis* lays its eggs singly on the hairs around the lips: the larvæ attach themselves to the stomach-wall, eventually migrating to the rectum, where they become re-attached. Before leaving the host they again become attached close to the vent and protrude therefrom. In all three species the larvæ are ultimately voided through the anus and pupate in the ground.

Among general works on the Œstridæ the original monograph of Brauer (1863) is important, together with the more recent treatises of Bau (*Genera Insectorum, Muscaridæ, Œstrinæ*, 1906) and of Seguy (1928).

Section C. PUPIPARA

A remarkable group of Diptera whose structure has been greatly modified in accordance with an ectoparasitic life. The winged forms do not fly any considerable distance, and all species are adepts at clinging to their hosts and working their way among the hairs or feathers. The claws are highly developed, and toothed or spined for the purpose. The abdomen is indistinctly segmented and, like the rest of the body, tough and leathery. With the exception of *Braula* all species are blood-sucking ectoparasites of mammals and birds, but do not utilize man as a normal host. The larvæ (excepting those of *Braula*) are retained within the uterus of the parents, where they are nourished by the secretion of the greatly developed accessory glands. When fully mature they are deposited on the ground, or in the abodes of their hosts, and almost immediately change to pupæ. A list of the palæarctic species arranged according to their hosts is given by Becker and Bezzi (1895). For the structure of the proboscis vide Muggenberg (1892) and Jobling (1926–28), and for the general biology and morphology of the family consult Massonnat (1908) and Falcoz (1926). The phylogeny and distribution is discussed by Speiser (1908) who has also monographed the world's genera. The group owes its existence more especially to the similarity in reproduction and parasitic habits exhibited by the adults. In all probability they are to be regarded as degraded members of the Schizophora.

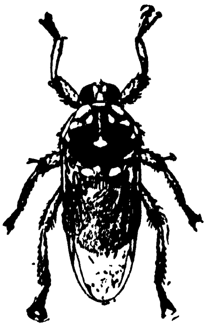
Fig. 618. — *Hippobosca rufipes.* × 2. S. Africa.

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FAM. HIPPOBOSCIDÆ.—HEAD SUNK INTO AN EMARGINATION OF THE THORAX. PALPI NEITHER LEAF-LIKE NOR FORWARDLY PROJECTING, FORMING A SHEATH TO THE PROBOSCIS. EYES ROUND OR OVAL, OCELLI PRESENT OR ABSENT. ANTENNÆ INSERTED INTO A DEPRESSION, 1-JOINTED, WITH OR WITHOUT A TERMINAL BRISTLE OR LONG HAIRS. LEGS SHORT AND STOUT, CLAWS STRONG AND OFTEN TOOTHED. WINGS PRESENT OR ABSENT.

These insects (Fig. 618) are dorso-ventrally flattened and of a tough leathery consistency, both features being correlated with an ectoparasitic life. The family includes such well known insects as the " forest fly " *Hippobosca equina* which affects horses and cattle, and the sheep " tick " or " ked " *Melophagus ovinus*. Among other British species *Ornithomyia avicularia* is a parasite of many wild birds and *Lipoptena cervi* is found on deer. All these species have a very extensive geographical range and *O. avicularia* has been carried by birds almost all over the world. The degree of development of the wings differs greatly in various members of the family. In *Hippobosca* and *Ornithomyia* they are fully formed : in *Allobosca* they are vestigial while in *Melophagus* (Fig. 619) wings and halteres are absent. Both sexes of *Lipoptena cervi* are winged but upon discovering a host the females soon cast their wings near the bases : wingless males similarly occur. The palpi in this family are rigid organs projecting forwardly downwards and forming a partial sheath to the proboscis. The latter is curved and slender, protrusible, and hidden from view when retracted. Whether both sexes are equally active bloodsuckers does not appear to have been definitely ascertained, but their punctures are seldom painful. The females produce at intervals single larvæ which are whitish, or pale yellow, with a black cap at the posterior end which involves the spiracles. They are immobile with little or no traces of segmentation, and very soon transform into puparia. For the genera of the family consult Speiser (1899) and an account of the structure of *Melophagus* is given by Pratt (1893) : the British species are discussed and figured by Austen (1903).

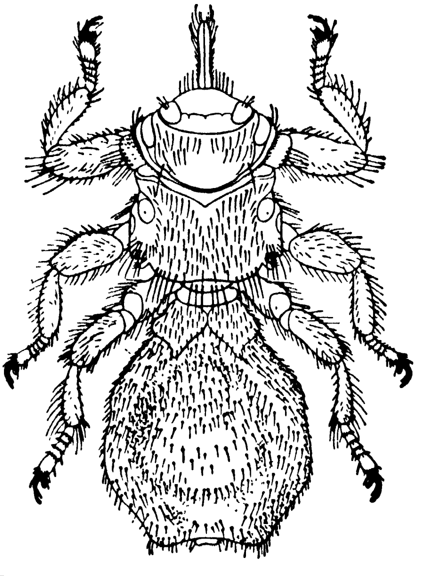
Fig. 619.—*Melophagus ovinus*, Magnified.

FAM. NYCTERIBIDÆ.—HEAD FOLDED BACK AT REST IN A GROOVE ON DORSUM OF THORAX, EYES AND OCELLI WHEN PRESENT VESTIGIAL ; ANTENNÆ 2-JOINTED, TERMINATED BY BRISTLES INSERTED ON TUBERCLES. A FAN-SHAPED COMB OF

BRISTLES (CTENIDIUM) INSERTED IN A HOLLOW AT THE ANTERIOR END OF THE THORAX; LEGS ELONGATE, WINGS ABSENT.

A very small family of highly modified and completely apterous insects (Fig. 620) parasitic upon bats. They are more particularly characteristic of the Old World, the countries bordering on the Indian Ocean being especially rich in species, only *Nycteribia* is British. In view of their host's power of distribution it is not surprising that certain species have a very wide geographical range. Frequently, a single species of Nycteribid may utilize several species of host which may be of different genera or, more rarely, of different families. Conversely a species of bat may support several species of Nyceteribids: thus, at least 9 species of the latter have been recorded from *Miniopterus schreibersi* in various countries. Information on the general structure and classification of the family is given by Speiser (1900A): the papers of Kolenati (1863) and Scott (1917) should also be consulted. Rodhain and Bequært (1916A) have published a detailed account of the behaviour of *Cyclopodia greefi* Karsch. The larvæ are deposited in a less advanced stage of development than those of certain Hippoboscidæ and the spiracles are postero-dorsal in position. The puparia were found adhering to the perches and parts of the cages in which the hosts were confined. According to Muggenberg (1892) a ptilinum is wanting in this family.

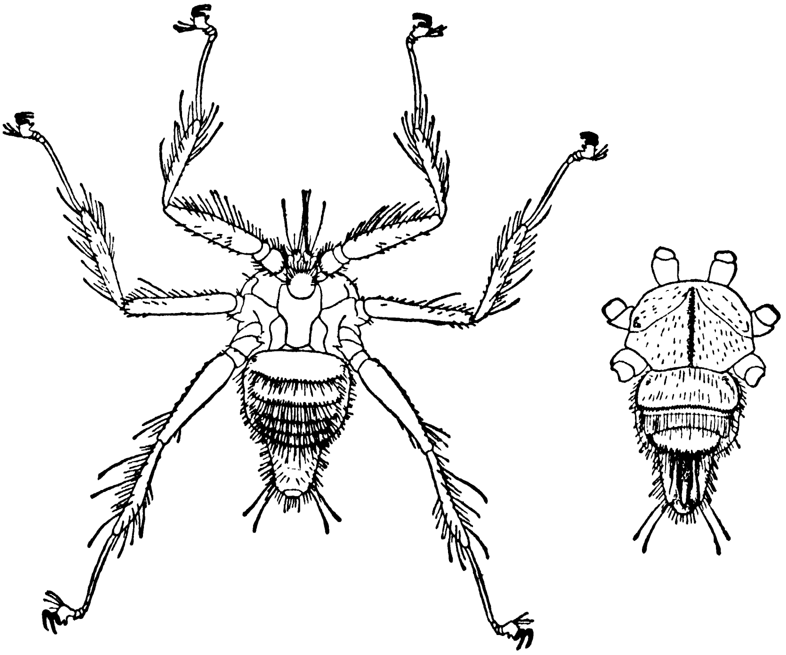

FIG. 620.—*PENICILLIDIA JENYNSI*, FORMOSA; DORSAL VIEW OF MALE WITH VENTRAL VIEW OF THORAX AND ABDOMEN ON RIGHT. ENLARGED.

FAM.. STREBLIDÆ.—HEAD NOT FLEXED ON DORSUM OR THORAX; EYES WHEN PRESENT SMALL, NO OCELLI; ANTENNÆ IN PITS, 2-JOINTED. PALPI LEAF-LIKE, PROJECTING IN FRONT OF THE HEAD BUT NOT SHEATHING THE PROBOSCIS. HIND COXÆ ENLARGED, CLAWS NOT DISTINCTLY TOOTHED. WINGS WELL DEVELOPED, VESTIGIAL OR ABSENT.

A small family widely distributed throughout the tropics and warm regions of the world. In habits they are almost exclusively parasitic upon bats, and most of what is known concerning the family is included in a paper by Speiser (1900). *Ascodipteron* Adens. (Queensland, E. Indies) is one of the most remarkable of Pupipara and is unique on account of the degeneration undergone by the female. Both sexes are winged but exhibit marked differences in the structure of the proboscis: in the female the labellar teeth are very large and blade-like, on the other hand, in the male, the teeth are exceedingly small. On reaching its host (*Minopterus*) the female makes a way beneath the skin near the base of the ear, and casts both legs and wings. In this situation she develops into a greatly enlarged, flask-shaped sac, with the hinder extremity communicating with the exterior (Muir, 1912). Typical genera of the family include *Nycteroboscα* Speis. which extends into Europe, *Raymondia* Frfld. and

Strebla Wied. Very little is known concerning their biology but Speiser states that they are larviparous.

FAM. BRAULIDÆ.—MINUTE LOUSE-LIKE INSECTS WITH SHORT THICK LEGS, VESTIGIAL EYES, AND DEVOID OF WINGS AND HALTERES. THE LAST TARSAL JOINT FURNISHED WITH A PAIR OF COMB-LIKE APPENDAGES.

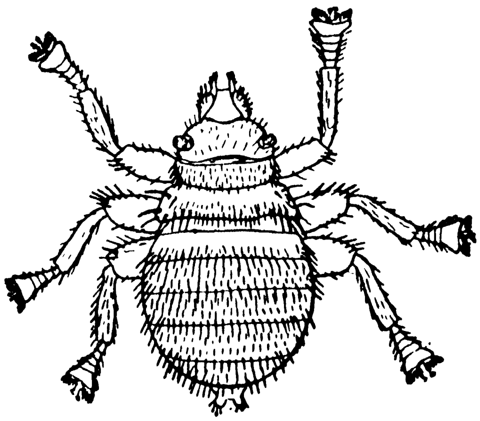

FIG. 621.—*BRAULA CŒCA.* × 24. *After* Carpenter.

Included herein is the single genus *Braula* Nitz. which lives in beehives. The species *Braula cœca* Nitz. (Fig. 621) is usually found clinging to the thorax of the queens and workers, but Dubini states that he has seen queens almost entirely covered with this parasite. The external structure of this remarkable creature has been studied to some extent by Meinert (1890, p. 216) and Börner (1908). According to Muggenberg (1892) a ptilinum is present and the mouth-parts agree in their essential morphology with those of the Hippoboscidæ. *Braula* is oviparous and according to Skaife (*Trans. Roy. Soc. S. Africa,* 1921) the eggs are laid among the brood combs. They hatch out into musciform larvæ which tunnel through the capped cells of the comb but do little harm. Pupation takes place in the cells and the imagines find their way to the bodies of the bees. The systematic position of this family is extremely doubtful and in some respects it appears to be allied to the Phoridæ.

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Vide also **SMITH, 1931,–A** Textbook of Agricultural Entomology. **Cambridge.**

Order 23. APHANIPTERA (Siphonaptera : Fleas)

SMALL, APTEROUS, LATERALLY COMPRESSED INSECTS WHOSE ADULTS ARE ECTOPARASITES OF WARM-BLOODED ANIMALS. EYES PRESENT OR ABSENT: ANTENNÆ SHORT AND STOUT, REPOSING IN GROOVES: MOUTH-PARTS MODIFIED FOR PIERCING AND SUCKING, MAXILLARY AND LABIAL PALPI PRESENT. THORACIC SEGMENTS FREE: COXÆ VERY LARGE, TARSI 5-JOINTED. LARVÆ ELONGATE, ERUCIFORM AND APODOUS. PUPÆ EXARATE, ENCLOSED IN COCOONS.

The Aphaniptera, or fleas, may be readily distinguished from other apterous parasitic insects since they are strongly compressed laterally instead of being dorso-ventrally flattened. They constitute a very sharply defined order of insects quite devoid of close connection with any other group. Their origin is very obscure, as no undoubted traces of wings have been discovered in any stage of their existence, and their general structure, although specialized in some directions, is simplified in others. They are presumed to have arisen from far-off winged ancestors but all traces of such descent have been deleted, and the simplifications of structure which they exhibit seem to suggest that their origin may have been relatively low down in the endopterygote series. In their metamorphoses they possess certain features in common with the Diptera Nematocera.

Fleas are blood-sucking ectoparasites of mammals and birds. They are negatively heliotropic and respond to warmth: when a host dies the fleas leave as soon as the body cools and seek fresh hosts which are not always of the same species. Many kinds are apparently confined to one species of animal while others infest a range of hosts. The relation between different species of fleas and their hosts, however, is not a very close one, and in the absence of the elective species of the latter, many will feed readily on the blood of other animals. Their powers of walking are slight, their chief method of progression being by leaping. According to Mitzmain the maximum vertical height attained by the leap of *Pulex irritans* is 7¾ inches, while the horizontal range may extend to 13 inches.

About 800 species of the order have been described of which 46 are known to occur in the British Isles (vide Rothschild, 1915). During the past twenty-five years the work of the Indian Plague Commission, and of many independent observers, has resulted in a great increase of knowledge relating to these insects. At least eleven species have proved capable of transmitting bubonic plague. In India the species mostly implicated is the rat-flea, *Xenopsylla cheopis* (Fig. 622). The rat is particularly susceptible to this disease, and the flea itself becomes infected with the plague bacillus by feeding upon an infected animal. When the latter dies, the fleas desert the body, and many find their way to man, particularly when the human population lives under crowded conditions in rat-infested quarters. It is impossible here to detail the evidence as to the manner in which the rat flea transmits the disease to man as the problem is a complicated one. It may be pointed out, however, that while feeding, the contents of the gut of the flea, which contain the pathogenic bacilli, are voided from time to time. This excretory matter, if it be introduced beneath the skin by scratching or other means, is liable to produce infection. Bacot and Martin have demonstrated that plague-infested fleas may convey the disease by a method comparable to inoculation. When placed on a host they suck vigorously but owing to the fact that, in a certain number of the insects, the digestive canal is blocked by a dense mass of rapidly multiplying plague bacilli, the blood that is imbibed fails to enter the stomach and is regurgitated into the puncture. Since this blood is now contaminated with bacilli derived from the previous host, the disease is thus transmitted to the new host. Rats are not the only animals attacked by plague, squirrels and other rodents being also liable to the disease; consequently fleas of any species, which attack both ground rodents and man, in lands where plague is prevalent, are to be regarded as possible agents in the transmission of the malady.

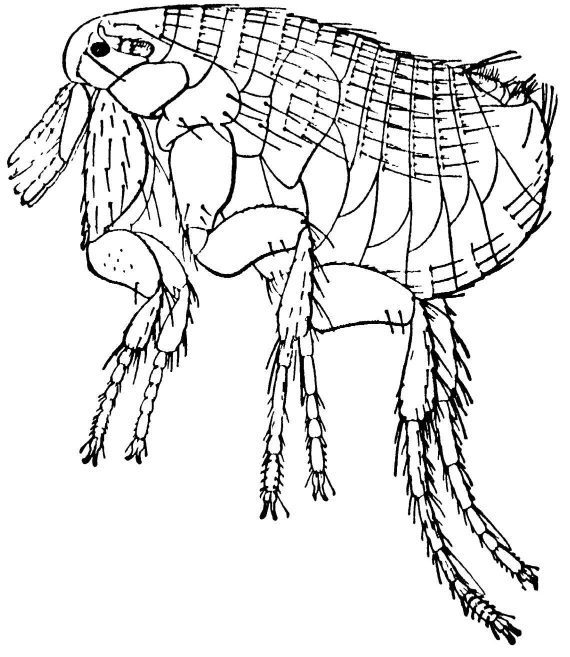

FIG. 622.—*XENOPSYLLA CHEOPIS*, MALE. × 20.

After Waterston. Reproduced by permission of the Trustees of the British Museum.

One of the most familiar of these insects is the cosmopolitan human flea *Pulex irritans*. Although man is its favourite host it is often found on the badger, also on the fox and other mammals. The extensive genus *Xenopsylla* includes the plague flea *par excellence* (*X. cheopis*) which has been previously alluded to: it is almost tropicopolitan and is a scarce vagrant in the British Isles. *Ctenocephalus* (Fig. 623) includes the dog and cat fleas (*C. canis* and *C. felis*) both of which occur on dogs and cats. The rabbit flea (*Spilopsyllus cuniculi*) commonly affects the ears of hares and rabbits, and sometimes becomes transferred to cats while the latter are hunting those animals. The genus *Ceratophyllus* includes a number of species, some affecting birds and others mammals. Of the former, *C. gallinæ* is frequent in hen-houses and in the nests of many wild birds: *C. penicilliger*, among the mammal-infesting forms, is common on numerous hosts including voles, mice, and stoats, while *C. fasciatus* is the common rat flea of cool countries. *Leptopsylla musculi* is harboured by the mouse and species of *Nycteriopsylla* and *Ischnopsyllus* are essentially bat parasites. In addition to the foregoing species, which occur in Great Britain, mention needs to be made of the well known "jigger" or "chigœ" (*Dermatophilus penetrans*) of the tropics whose females remain attached to the skin in one position for the greater part of their existence. The modifications of external structure associated with this habit are so marked that the abdomen becomes distended to the size of a small pea, the insect bearing a close resemblance to a tick. It has a large number of hosts and its attacks are usually confined to the feet: in man it particularly affects the toes. Instead of remaining at the surface of its host, the fertilized female burrows into the flesh, until it may become completely embedded.

External Anatomy.—The body in the Aphaniptera is strongly compressed, and well chitinized, with the evident advantage of enabling these insects readily to work their way among the hair or feathers of the host. There is usually a prominent armature of spines and bristles which are sharply inclined backwards, thus aiding forward progression, and the claws of the feet are strong in conformity with the necessity for grasping. The *head* is very closely attached to the thorax without the intervention of a cervicum. Situated on the middle line of the frons there is, in many species, a chitinous tubercle which probably functions as an organ for the imago to cut through the pupa case and cocoon during emergence. The *eyes* are non-faceted, and may be deeply pigmented but, in a number of species, they are vestigial or absent. The latero-ventral border of the head often carries a row of powerful spines forming the *genal comb* which is present on either side: these organs are frequently referred to as ctenidia and are well seen, for example, in *Ctenocephalus*. The *antennæ* are lodged in antennal grooves and are short and stout with three evident joints. The terminal portion is pectinated and exhibits a number of annular divisions, which vary in completeness of development in different genera, and sometimes in different sexes. The *mouth-parts* (Fig. 624) are adapted for piercing and sucking, and the most important organs are the *mandibles*. These structures are rather broad blades which are serrated along the distal two-thirds of their length. Proximally, the inner surfaces of the mandibles are in contact with the short hypopharynx and, where the latter organ terminates, they are closely opposed to the epipharynx above. Each mandible is distally grooved along its inner aspect from the point where the hypopharynx ceases, and they form together a channel through which the saliva is ejected. Basally, the mandible articulates with the head capsule by means of a small rod-like sclerite which imparts to it considerable freedom of movement. The *labrum-epipharynx* is a long slender organ which is ventrally grooved, and closely approximated to the mandibles, the combined organs thus forming an afferent channel through which blood is sucked up. The *hypopharynx* is a small sclerite which is concave ventrally and incurved at the

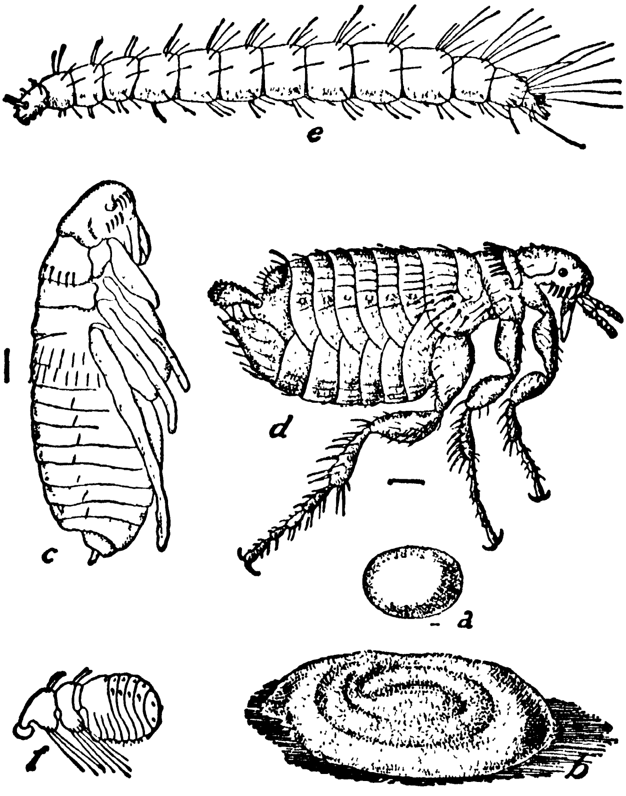

FIG. 623.—*CTENOCEPHALUS CANIS.*

a, egg; *b*, larva in cocoon; *c*, pupa; *d*, imago; *f*, antenna of imago; *e*, *Ceratophyllus fasciatus*, larva. From Bishopp, *U. S. Dept. Agric. Ent. Bull.* 248 (all except *e*, *after* Howard).

margins: within the area thus defined the salivary pump and its operating muscles are lodged. Anteriorly, the hypopharynx is prolonged into a small process, which is perforated by the salivary duct, and extends for a short distance between the epipharynx and the mandibles. The *maxillæ* each consist of a single lobe or blade, on either side of the mouth, and a 4-jointed palpus: they are not cutting organs and apparently do not enter the puncture made by the mandibles. The *labium* is formed of an oblong basal plate or mentum, which carries distally a pair of labial palpi: the latter are elongate and usually 5-jointed but the number of joints varies between 2 and 17. In transverse section the labial palpi are slightly concave and, when placed together, they form a kind of sheath which encloses the piercing mouth-parts. When a flea desires to feed it punctures the skin by means of the combined piercing organ formed by the labrum-epipharynx and mandibles. The muscles of the salivary pump inject saliva into the perforation thus formed and the aspiratory action of the pharynx draws up blood from the now congested wound, through the afferent channel, and so into the stomach. Considerable difference of opinion exists as to whether the labrum-epipharynx exercises any piercing function at all: several observers maintain from the structure of its apex that it is incapable of perforation and, if this view be the correct one, it is evident that the wound is made solely by the mandibles.

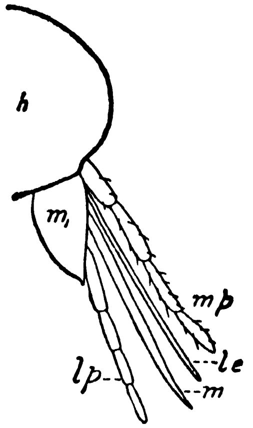

FIG. 624.—DIAGRAM OF THE MOUTH-PARTS OF A FLEA.

h, head; *le*, labrum-epipharynx; *lp*, labial palp; *m*, mandible; m_1, maxilla; *mp* maxillary palp.

The *thorax* is composed of three quite distinct segments which admit of a certain amount of movement. In many species the hind margin of the pronotum carries a row of stout spines forming the *pronotal comb*. The terga are simple, broad, arched plates and the metathorax is characterized by its greatly developed epimera which overlie the base of the abdomen. The legs are adapted for clinging and leaping with large flattened coxæ, short stout femora and elongate 5-jointed tarsi.

The *abdomen* is composed of 10 segments, the first of which has the sternum wanting, and the last three segments are modified for sexual purposes. The ninth segment in the male is of a complex nature. Its tergum bears a dorsal *sensory plate* or *pygidium* and the sides of the former region are modified to form accessory copulatory organs or claspers. The ninth sternum is represented by a pair of boomerang-shaped sclerites each of which consists of an internal vertical and a ventral horizontal arm, the latter projecting beyond the eighth sternum. The *penis* is an organ with complex chitinous parts projecting between the clasping organs and the ninth sternum. The tenth segment is greatly reduced and represented by two small plates, one above and the other below the anus. In the female the terminal segments are less modified than in the male. The ninth tergum similarly carries a dorsal sensory plate while the sternum of that segment forms the ventral wall of the vaginal cavity. The tenth tergum consists of a small plate bearing a conical setiferous process known as the *stylet* and the corresponding sternum is represented by a small ventral plate.

Internal Anatomy.—What may be regarded as the mouth is situated at the base of the epipharynx and forms the definitive opening into the alimentary canal. The first region of the latter is the pharynx which is an elongate chamber with strongly chitinized dorsal and ventral walls. In virtue of its powerful dilator muscles the pharynx functions as a pumping organ for imbibing blood from the host. It is followed by a long œsophagus of very small calibre, which leads into a somewhat conical organ termed the proventriculus. The inner walls of the latter are beset with a series of long backwardly directed chitinous rods. The function of this arrangement appears to be to prevent the regurgitation of the stomach contents when the pharynx is dilated in the act of sucking. The stomach, when fully distended, occupies a large part of the abdominal cavity and, near its junction with the hind intestine, are found the insertions of the four Malpighian tubes. Near the termination of the hind intestine there are six rectal papillæ resembling those found among Diptera. The *salivary glands* consist of a pair of ovoid sacs on either side: their ducts eventually combine to form a common canal which enters the salivary pump beneath the hypopharynx. The *nervous system* [1] is exceptionally primitive in that the ventral nerve cord consists of three thoracic and seven abdominal ganglia: these centres are very much approximated owing to the great reduction in length of the intervening connectives. The *male reproductive organs* consist of a pair of fusiform testes whose contents pass down extremely fine vasa deferentia: the latter unite to form a single passage opening into a small vesicula seminalis. The ejaculatory duct is associated with a copulatory organ of complex structure. The *female reproductive organs* are composed of a pair of ovaries, each formed of from four to eight panoistic ovarioles. Attached to the vagina there is a strongly chitinized spermatheca whose shape and size differ among various species. The *respiratory system* is well developed and communicates with the exterior by ten pairs of spiracles: two pairs of the latter are located on the thorax, the remainder being abdominal in position.

Biology and Metamorphosis (Fig. 623).—The eggs of these insects are ovoid and white or cream in colour: unlike those of many ectoparasites they are not glued to the hair or feathers of the host. When deposited on the body of the latter they readily fall off and are normally found in the haunts or sleeping-places of the animal parasitized. In houses fleas breed in the cracks of floors, under matting or beneath carpets and almost always in uncleanly dwellings. Rat fleas often breed in granaries, barns, etc., particularly in those where there is an accumulation of floor litter. The dried excrement, feathers, straw, etc., which accumulate in chicken houses also afford a favourable environment. The incubation period varies on an average from three to ten days, according to temperature, and the young larva ruptures the chorion by the aid of a hatching-spine on the dorsal side of the head. The larvæ (vide Bacot and Ridewood, 1914: Sikes, 1930) are active, whitish, vermiform objects usually measuring about 4 mm. in length when fully grown. They are non-parasitic and feed upon particles of organic matter found in the host's lair, or among the dust and dirt which collects on the ground in the vicinity. In some species, however, blood which has passed through the body of adult fleas appears to be a necessary part of their nutriment. Larval Aphaniptera possess a well developed head but are devoid of both eyes and legs: in their general characters they resemble the larvæ of certain Nematocera. The antennæ are single-jointed but rather prominent, the mandibles are very definitely toothed and the maxillæ assume a curious brush-like form with small 2-jointed palpi: each

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[1] According to Minchin (1915) there are seven abdominal ganglia in the female of *Ceratophyllus fasciatus* and eight in the male.

labial palp is composed of a short basal joint surmounted by stout setæ. The trunk consists of three thoracic and ten abdominal somites, each of which is armed with a band of outstanding bristles. Spiracles are present on the thorax and first eight abdominal segments. After undergoing two ecdyses, the larva spins a cocoon which is concealed by the fine particles of débris adherent to its outer surface. The adults remain quiescent for a variable period before emerging from the cocoons, and they often issue in large numbers in response to slight mechanical stimuli. The vibrations set up by persons walking about a disused room, for example, have been explained as being the cause of the emergence of an abundance of fleas within a very short time. When newly emerged, the adults can remain alive for a considerable period without food, but they take the first opportunity of reaching their particular host. As a general rule the female needs to imbibe the blood of the normal host before becoming capable of laying fertile eggs.

The period occupied by the complete developmental cycle varies in different species and in different countries. Thus *Pulex irritans* in Europe requires from 4 to 6 weeks while *Xenopsylla cheopis* in India passes through a complete generation in about 3 weeks: on the Pacific coast the life-cycle of the latter species occupies, according to Mitzmain, 9 to 11 weeks.

Classification.—The order may be divided into three well-defined families as follows:—

1. Thorax shorter than 1st abdominal segment, mid-dorsally; metathoracic epimera extending well beyond 1st abdominal segment; maxillary palpi longer than fore coxæ: mature female with greatly dilated abdomen and living beneath skin of host. *Dermatophilus* (*Tunga*), *Echidnophaga*.	DERMATOPHILIDÆ (Sarcopsyllidæ)
2. Thorax longer than 1st abdominal segment, mid-dorsally; metathoracic epimera not extending beyond 1st abdominal segment; maxillary palpi mostly shorter than fore coxæ; species roaming freely over hosts.	
3. Maxillæ clubbed or subquadrangular; species found on bats. *Ceratopsylla*.	CERATOPSYLLIDÆ.
4. Maxillæ triangular with apices acute; species not found on bats. *Pulex, Ctenocephalus, Xenopsylla,* etc.	PULICIDÆ.

Literature on Aphaniptera

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Vide also " Reports on Plague Investigations in India," published in *Journ. Hyg.* between 1905 and 1914: also textbooks of parasitology and medical entomology.

ADDENDA

P. 74. Tarsal gustatory sense.—Sensillæ, that are presumably tarsal chemoreceptors, are described by Eltringham in Lepidoptera (*Trans. Roy. Ent. Soc.* 81, 1933).

P. 125. Blood Gills.—Recent experimental observations by Thorpe (*Ve Cong. Internat. Ent. Paris*, 1933) lead to the conclusion that these organs perform no significant part in respiration.

P. 176. Embryonic envelopes.—In the Braconid *Dinocampus* (*Perilitus*) *rutilus*, D. J. Jackson (*Proc. Zool. Soc.* 1928, p. 617) has shown that when the larva issues from the egg the trophamnion cells become dispersed in the hæmocœle of the host. They assume a globular form, markedly increase in size through the absorption of fatty material, and form the principal food of the larva in its later instars. If the parasite happens to die the trophamnion cells continue to grow and may attain an abnormally large size.

P. 251. Phase Theory.—In Fig. 259 the tarsi should be represented with three joints.

P. 409. Mecoptera.—According to Mercier (1915) the salivary glands of *Panorpa* attain much greater development in the male than in the female. This feature is correlated with the secretion, in the male, of a globule of saliva. The latter is discharged on the ground and, while it is being imbibed by the female, pairing takes place.

P. 434. Scales of Lepidoptera.—For the development of these structures, see also Reichelt (*Zeits. f. Morph. u. Ökol.* 3, 1925).

P. 548. Hymenoptera.—In Fig. 524 the maxillary palpus is six-jointed, a joint having been omitted.

P. 573. Braconidæ.—For a list of the British species of the family, see Lyle (*Trans. Roy. Ent. Soc.*, 1933).

P. 607. Andrenidæ.—The researches of Stockhert (*Konowia*, 2, 1923) show that certain species of *Halictus* are truly social. Thus, *H. malachurus* has a sterile worker caste of smaller size than the parent and differently sculptured. Individuals of this type have been referred by taxonomists to a separate species, *H. longulus*; they provision the nest and die at the end of the season. Fertile females of the *malachurus* type appear in August and over-winter, founding new nests in spring. The males are of the *malachurus* type also; they eagerly pair with the young females of their own type and not with the *longulus* females.

P. 639. Nematocera, Fam. Nymphomyiidæ.—In *Annotationes Zoologicæ Japonenses* (13, pp. 559–66, pl. 34, 1932), Tokunaga describes a new genus and species of Diptera based upon six examples taken along a torrential stream in Kyoto. This new type (*Nymphomyia alba*) has been submitted to English and American specialists and there seems no question that it represents a hitherto unknown family to which the name Nymphomyiidæ is given. The head is prognathous, there are no trophi and the compound eyes are contiguous ventrally: the antennæ are 5-jointed and of the brachycerous type. The abdomen is extremely elongated and 9-segmented while there are no spiracles on either the thorax or the abdomen. The legs are characterized by the extremely elongated coxæ and trochanters. The wings are longer than the whole body and are fringed with long setæ very much as in the Thysanoptera, with the venation very much reduced: the halteres are also very long. In its general characters this remarkable creature seems to bear a remote likeness to the Psychodidæ and Cecidomyiidæ. It is evidently a member of the Nematocera, although the antennæ are totally different from the prevailing type among that group. The author promises more detailed studies that are to be published in the Memoirs of the Kyoto Imperial University.

P. 654. Leptidæ.—For a most interesting account of the structure and biology of *Vermileo*, and a comparison with similar behaviour in larvæ of the Myrmeleonidæ, see the book by Wheeler entitled "Demons of the Dust" (London: 1931).

P 654. Pantopthalmidæ.—For a detailed study of the larval and adult structure of *Pantopthalmus*, see Thorpe (*Trans. Roy. Ent. Soc.* 82, 1934).

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